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A Review of *Peroryctes broadbenti*, the Giant Bandicoot of Papua New Guinea

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ABSTRACT

The giant bandicoot, *Peroryctes broadbenti* (Ramsay, 1879), is represented in museum collections by 23 specimens collected at 12 localities in the lowlands of the southeastern peninsula (the "Papuan Peninsula") of Papua New Guinea. Available data on *P. broadbenti* are reviewed, including its comparative anatomy and morphological variability, taxonomic relationships, geographic and elevational distribution, dietary and reproductive traits, and conservation status. Despite previous confusion between this species and *P. raffrayana* (Milne-Edwards, 1878), the two species are readily distinguished by a suite of external, cranial, and dental characters. Diagnostic characters are enumerated and illustrated, and comparisons drawn with other New Guinean bandicoots. Generic distinction of *Peroryctes* Thomas, 1906, in cranial morphology from other New Guinean bandicoots is also reviewed. A striking degree of sexual dimorphism is documented in both body size and dentition for *P. broadbenti*; these comparisons are set in context by a review of sexual dimorphism among bandicoots in general.

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INTRODUCTION

The marsupial fauna of mainland New Guinea includes four genera and at least 11 species of bandicoots, members of the order Peramelemorphia Ameghino, 1889 (sensu Aplin and Archer, 1987) (Kirsch, 1968; Groves and Flannery, 1990; Helgen and Flannery, 2004; Groves, 2005). All are terrestrial omnivores and most are small to moderate-sized mammals, with adults rarely exceeding 2 kg in body weight (Seebeck et al., 1990; Hume, 1999). The exception is the so-called giant bandicoot, *Peroryctes broadbenti* (Ramsay, 1879), a poorly known species of southeastern Papua New Guinea. Adult males of this species can attain weights well in excess of 4 kg (Flannery, 1995), and are larger than any other living or fossil bandicoot and more than twice the bulk of even the largest of the Australian bandicoots.

Although the giant bandicoot was first described in 1879, virtually nothing has been reported regarding its morphology, distribution, or ecology. One reason for this is longstanding confusion between *P. broadbenti* and a smaller-bodied congener, *Peroryctes raffrayana* (Milne-Edwards, 1878). Another is the limited representation of *P. broadbenti* in scientific collections—a situation that reflects its restricted geographic range and possibly natural rarity. In this article we review the taxonomy and distribution of *P. broadbenti,* and clarify the distinction between it and *P. raffrayana*. We also document the distribution and habitat associations of *P. broadbenti* based on the combined holdings of the world's museums.

Taxonomic History of *Peroryctes broadbenti*

The first specimen of the giant bandicoot was collected by Kendal Broadbent during an early foray inland from the newly established town of Port Moresby, on the southern side of New Guinea's southeastern peninsula (see fig. 1 for localities). Though the Australian zoologist E.P. Ramsay mentioned this specimen in a footnote to his review of the bird and mammal fauna of the Port Moresby area (Ramsay, 1878: 244), it was not until the following year that he named "this fine species" *Perameles broadbenti.* His description of the only specimen, an adult male represented by a preserved skin (subsequently mounted) and a complete skull, was relatively detailed and well illustrated (Ramsay, 1879). Ramsay was most likely unaware that three other New Guinean bandicoots had been named between 1875 and 1878 by systematists in Germany, Italy, and France (*Perameles rufescens* Peters and Doria, 1875 [= *Echymipera rufescens*], *Perameles longicauda* Peters and Doria, 1876 [= *Microperoryctes longicauda*], and *Perameles raffrayana* Milne-Edwards, 1878 [= *Peroryctes raffrayana*], all based on specimens collected in far western New Guinea). At any rate, his account did not include comparisons with these species or with the earlier named Australian bandicoots.

Thomas (1888) was the first to present a systematic treatment of all the then known bandicoots. He identified a "*raffrayana*" species group within *Perameles* and provisionally treated *broadbenti* as a distinct species alongside *raffrayana* and *longicauda.* However, he regarded *broadbenti* as "somewhat doubtful, judging merely to the original description and figures, to which alone I have had access" (1888: 241). Tate and Archbold (1937) listed *broadbenti* as a synonym of *raffrayana* but remarked that examined material of *P. raffrayana* "from Papua

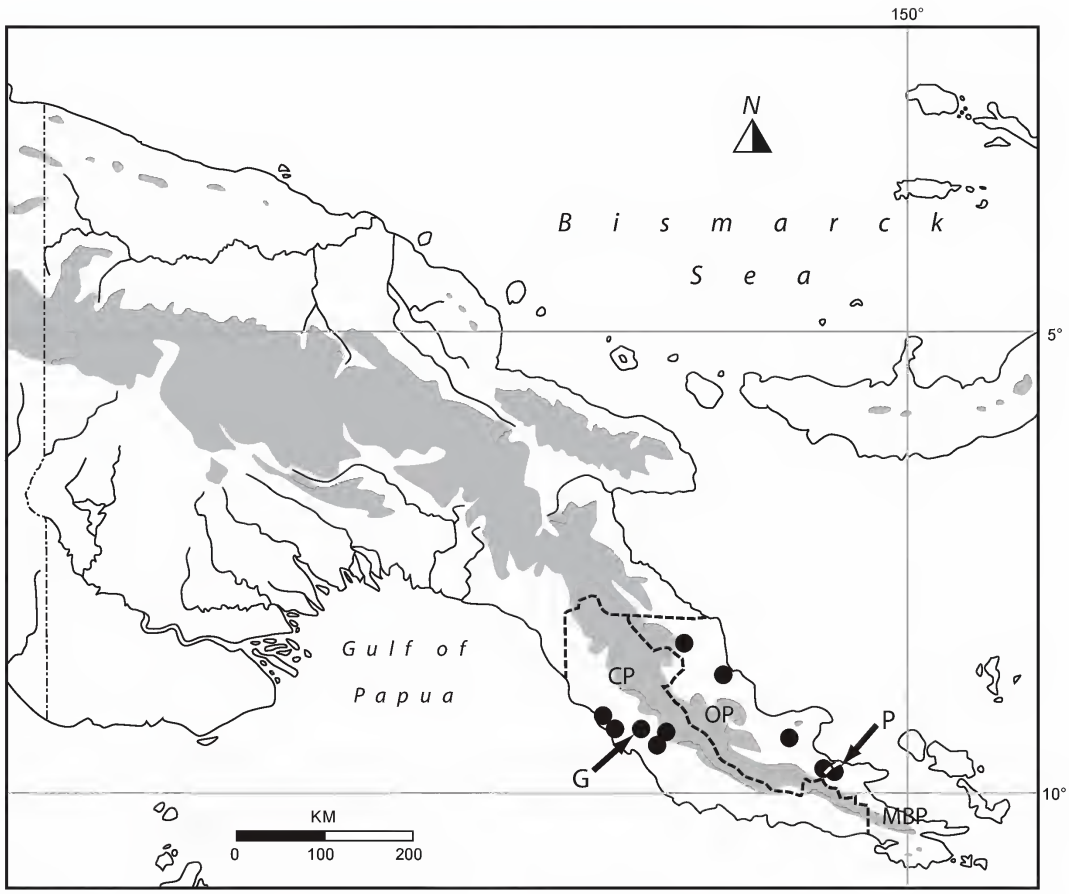

FIGURE 1. Map of southeast Papua New Guinea showing collection localities of *Peroryctes broadbenti* and boundaries of the three provinces that make up the "tail" of the island of New Guinea. CP = Central Province; MBP = Milne Bay Province; OP = Oro Province; G = Goldie River, type locality of *P. broadbenti*; P = Peria Creek, where the Fourth Archbold Expedition to New Guinea collected the largest available museum series of *P. broadbenti*. Areas above 1000 m in elevation are shaded in gray.

[= southeast Papua New Guinea] comprises mountain and lowland forms which are at once distinguishable by the quality of their pelage, the mountain form having comparatively long, woolly fur, the lowland animal thin, bristly hair which is essentially sparse beneath" (1937: 353). They remarked of the holotype of *P. broadbenti* that "apart from its unusually large size (which applies to the body and skull but not to the teeth) . . . [it] appears to have more nearly matched our lowland-dwelling form" (1937: 353–354), but conceded that Ramsay's description of the length and quality of the pelage was more consistent with their mountain form. According to a later remark by Tate (1948b), a specimen listed by Tate and Archbold (1937: 432) as *P. raffrayana* from the Weyland Range (AMNH 103254) in far western New Guinea was earlier regarded as a representative of *broadbenti*.

In a subsequent, more formal review of bandicoot systematics, Tate (1948b) combined all named forms of *Peroryctes* under two species, *raffrayana* and *longicauda,* each with three

subspecies. Within *raffrayana,* Tate now recognized three allopatric forms—typical *raffrayana* from western New Guinea, *broadbenti* in the southeast, and *rothschildi* (Förster, 1913) on the Huon Peninsula. He reported all three across wide altitudinal ranges, stating of *broadbenti* that it "extends as high as 2860 meters" (1948b: 327). Tate further commented that he could find "no dental difference whatsoever" between *broadbenti* and typical *raffrayana,* but noted that "the nasals in *broadbenti* appear slightly longer than those of either *raffrayana* or *rothschildi*" (Tate, 1948b: 327).

New material of *P. broadbenti* was obtained during the Fourth Archbold Expedition to southeast Papua (Brass, 1956), together with a good series of typical *P. raffrayana.* Based on this material, Van Deusen (1972; also Van Deusen and Jones, 1967) subsequently championed the recognition of *P. broadbenti* as a valid species, though he did not provide any specific information as to its morphology, distribution, or ecology. Despite the lack of published detail, *P. broadbenti* was henceforth credited as a full species in all major compendia of New Guinean mammals (Kirsch and Calaby, 1977; Ziegler, 1971, 1977; Flannery, 1990a, 1995; Menzies, 1991; Groves, 1993, 2005), albeit sometimes with qualification (e.g., Kirsch and Calaby, 1977). Flannery (1990a, 1995), George and Maynes (1990), and Menzies (1991) each gave a brief synopsis of the distribution and habits of the species, based on partial knowledge of museum holdings.

The generic arrangement of New Guinean bandicoots has undergone a number of significant revisions and these affect our understanding of the relationships of *P. broadbenti.* Thomas (1906) established the genus *Peroryctes* for a group of four species (*raffrayana, broadbenti, longicauda,* and *ornata* [Thomas, 1904]), distinguished from *Echymipera* Lesson, 1842, by having five rather than four upper incisors, the "lachrymal bone rounded externally" and the "braincase normal" (Thomas, 1906: 476). Stein (1932) introduced a third New Guinean bandicoot genus with the description of *Microperoryctes murina* Stein, 1932, a very small, unpatterned bandicoot from the Weyland Range of western New Guinea. Stein distinguished his new genus from *Peroryctes* mainly on its unusually small size (total length well below 300 mm). Tate and Archbold (1937) divided *Peroryctes* into two subgenera on the basis of external and cranial characters. The subgenus *Peroryctes* was restricted to *raffrayana,* with *broadbenti* and *rothschildi* as synonyms; a new subgenus (*Ornoryctes*) was erected for the smaller-bodied, variably ornate taxa (*longicauda* and *ornata*), despite noting that the skull of *Microperoryctes* "is essentially a miniature of that of *Peroryctes* (*Ornoryctes*)" (Tate and Archbold, 1937: 355). This generic arrangement was maintained by Tate (1948b) and followed by Laurie and Hill (1954), albeit with the addition of another small-bodied taxon from southeast Papua, *P. papuensis* Laurie, 1952 (= *Microperoryctes papuensis*; reviewed by Aplin and Woolley, 1993). Tate's generic arrangement was followed by Ziegler (1977) and Kirsch and Calaby (1977).

The most recent taxonomic changes affecting *P. broadbenti* began with Groves and Flannery's (1990) reassessment of craniodental and external morphological characters among all major groups of bandicoots. Their principal taxonomic conclusions for the New Guinean bandicoots were: (1) recognition of the endemic New Guinean bandicoots as a separate family (Peroryctidae) from the Australian Peramelidae; (2) restriction of the genus *Peroryctes* to *raffrayana* and *broadbenti*; and (3) inclusion of the smaller, patterned New Guinean bandicoots

(i.e., Tate and Archbold's *Ornoryctes*) within *Microperoryctes*. Groves and Flannery (1990) regarded *Peroryctes* as the most plesiomorphic of all living bandicoots and as a sister lineage to all other peroryctid bandicoots (*Microperoryctes* and *Echymipera* of New Guinea, and *Rhynchomeles* Thomas, 1920, represented by the single species *R. prattorum* Thomas, 1920, endemic to the Moluccan island of Seram). Helgen and Flannery (2004) recently described a further species of *Microperorytes* (*M. aplini*) and tentatively advocated maintaining *Ornoryctes* at subgeneric level for the striped mouse-bandicoots.

Support for the Groves and Flannery arrangement was forthcoming from two early genetic studies, one using the method of microcomplement fixation of albumin (Baverstock et al., 1990), and the other using the method of DNA-DNA hybridization (Kirsch et al., 1990). Later studies of 12SrRNA mitochondrial gene sequences (Westerman et al., 1999, 2001; Pacey et al., 2001) failed to identify a monophyletic Peroryctidae; instead, these results identified *Peroryctes raffrayana* as a sister lineage to all other peramelids and peroryctids, thereby rendering Peroryctidae paraphyletic. Groves (2005) took these molecular findings into account when formulating the most recent taxonomic classification of bandicoots. He divided Peramelemorphia into three families: Thylacomyidae for *Macrotis* Reid, 1837, Chaeropodidae for *Chaeropus* Ogilby, 1838, and Peramelidae for all other genera; and further divided Peramelidae into three subfamilies: Peroryctinae for the genus *Peroryctes,* Echymiperinae for *Echymipera, Microperoryctes,* and *Rhynchomeles,* and Peramelinae for *Perameles* É. Geoffroy, 1803, and *Isoodon* Desmarest, 1817. The most recent published study of bandicoot phylogenetic relationships, drawing on a six-kilobase concatenation of protein-coding regions from five nuclear genes (Meredith et al., 2008) supported the concept of a monophyletic Peroryctidae (i.e., a sister relationship between Echymiperinae [as represented in the study by species of *Echymipera* and *Microperoyctes*] and Peroryctinae [as represented in the study by *Peroryctes raffrayana*]). Neither *Peroryctes broadbenti,* the subject of this review, nor *Microperoryctes murina,* the type species of *Microperoryctes,* have been represented in any published molecular studies.

Materials and Methods

External measurements were taken from museum labels; most were taken on live or freshly killed specimens by the original field collectors. Linear measurements are in millimeters (mm), weights in kilograms (kg) or grams (g). Craniodental measurements, except as noted, were taken by the authors with handheld calipers; their limits are illustrated in figure 2. Not all cranial measurements were taken on every specimen. Those without a full measurement set were examined by Helgen during visits to various collections in Europe and Papua New Guinea prior to the start of our more detailed studies of *Peroryctes.*

Cranial terminology follows that illustrated for a didelphid marsupial (*Monodelphis brevicaudata* [Erxleben, 1777]) by Wible (2003). Terminology of cusps and other features on upper and lower molars follows Turnbull et al. (2003). Dental enumeration follows Luckett (1993; see also Luckett and Woolley, 1996) in recognizing the four adult molars as M1–4. However, while Luckett (1993) showed convincingly that the first two premolars of adult bandicoots are

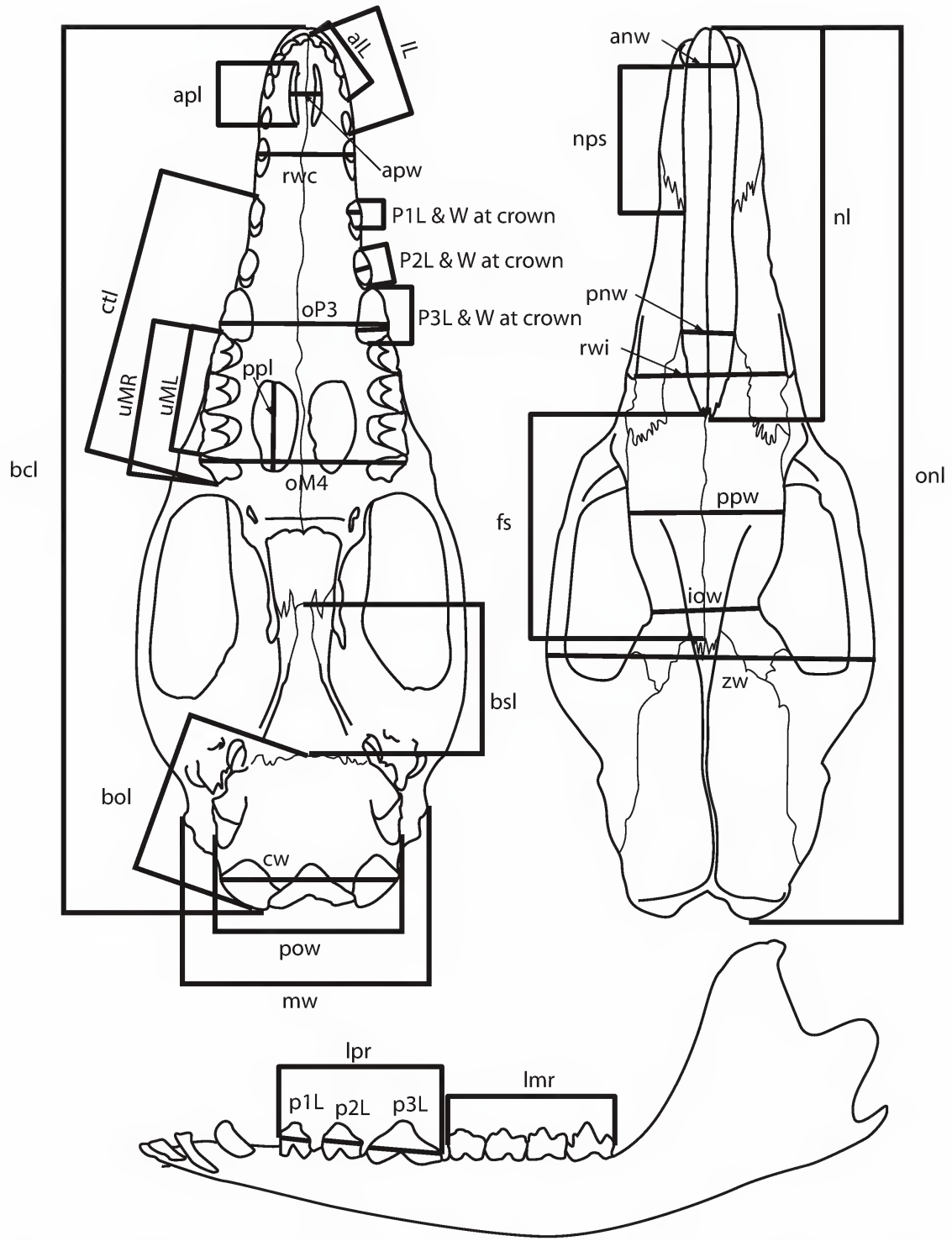

FIGURE 2. Cranium and dentary of an adult male *Peroryctes broadbenti* showing the limits of the cranial and dental measurements used in this study (see Materials and Methods for abbreviations and definitions).

unreplaced deciduous teeth (i.e., dP1 and dP2) contrasted with a replacement tooth in the third position (i.e., P3), we maintain prior usage and designate the adult premolar series on a purely positional basis as P1–3 (see fig. 2).

Abbreviations

Specimens discussed here are held in the collections of the Australian Museum, Sydney (AM), the American Museum of Natural History, New York (AMNH), the Bernice P. Bishop Museum, Honolulu (BBM), the Natural History Museum, London (BMNH), the Australian National Wildlife Collection, Canberra (CSIRO), the Naturhistorische Museum, Vienna (NMW), the Papua New Guinea National Museum and Art Gallery, Port Moresby (PNGNM), the South Australian Museum (SAM), and the Biology Department of the University of Papua New Guinea (UPNG).

The following abbreviations are used in various tables and figures:

aIL	Length of anterior upper incisor series (I1–4), measured at crown bases
apl	Length of incisive (anterior palatal) foramen
anw	Combined anterior width of the nasal bones
apw	Combined width across the paired anterior palatal foramina
bcl	Condylobasal length
bol	Length of basioccipital bone
bsl	Length of basisphenoid bone
ctl	Length of cheektooth series (premolars + molars)
cw	Combined width of occipital condyles
fs	Length of midline suture of frontal
IL	Length of entire upper incisor series (I1–5), measured at crown bases
iow	Width of greatest constriction of orbitotemporal fossa
lmr	Combined length of lower molar series (m1–4), measured at crowns
lpr	Combined length of lower premolar series (p1–3), measured at crowns
mw	Maximum width across braincase
nl	Maximum length of nasal bone
nps	Length of sutural contact between nasal bone and premaxilla
oM4	Palatal width, measured across anterolabial corner of each M4
onl	Greatest length of skull (occipitonasal length *or* occipitopremaxillary length)
oP3	Palatal width, measured across posterolabial corner of each P3
p1L	Length of p1, measured at crown
p2L	Length of p2, measured at crown
p3L	Length of p3, measured at crown
P1L	Length of P1, measured at crown
P2L	Length of P2, measured at crown
P3L	Length of P3, measured at crown
P1W	Width of P1, measured at crown
P2W	Width of P2, measured at crown
P3W	Width of P3, measured at crown
pnw	Combined posterior width of the nasal bones, measured at intersection with maxillofrontal suture
pow	Width across outside of paroccipital process
ppl	Length of posterior palatal foramen
ppw	Maximum width across postorbital ridge
rwc	Anterior rostral width, measured across outer surface of each canine
rwi	Posterior rostral width, measured across medial surface of each infraorbital foramen
uML	Combined length of M1–3, measured at crowns
uMR	Combined length of M1–4, measured at crowns
zw	Maximum width of cranium, measured across zygomatic arches

RESULTS

We located a total of 23 museum specimens of *P. broadbenti*. These specimens were distinguished initially from all examples of *P. raffrayana* by the following characteristics: (1) overall large size, especially of males; (2) presence of contrasting, reddish-brown fur on flanks; (3) absence of patches of white fur on venter; (4) paler manus and pes; (5) greater breadth of rostrum; and (6) hypertrophy of posterior upper and lower premolars in males. Many other craniodental differences were noted on closer study of representative series (see below).

Distribution of *P. broadbenti*

The 23 examples of *P. broadbenti* come from 12 localities in three provinces of Papua New Guinea (see fig. 1). Place names and altitudes were taken from skin tags or published expedition summaries. Gazetteers of New Guinea mammal collecting localities compiled by Bonaccorso (1998), Flannery (1995), Taylor et al. (1982), and Laurie and Hill (1954) were the principal references regularly consulted for geographic coordinates.

Central Province

1. Goldie River (09°16′S, 147°22′E): AM A3238, adult male, pre-1878, skull and mounted skin.
2. Brown River (09°15′S, 147°05′E): PNGNM 24028, adult female, 28 April 1970, skull only; PNGNM 23727, juvenile female, 30 May 1970, skin and skull; PNGNM 23726, juvenile male, 30 May 1970; skin and skull.
3. Sogeri (09°25′S, 147°32′E): PNGNM 23714, adult female, 1 July 1969; skin only.
4. Vanapa River (09°08′S, 146°58′E), PNGNM 23390, adult male, 25 September 1969, skin and skull; AMNH 222624, adult male, 30 August 1970, skull.
5. Hufeisengebirge (Mt. Maguli) (09°28′S, 147°37′E): NMW 109, adult male, 1902, skin and skull, collected by Carl Hunstein.
6. "Kariva-Veniarii Rivers" (exact locality uncertain): UPNG 557, adult male, 8 November 1970, skin and skull.
7. Koki Market, Port Moresby (i.e., purchased from a market, actual provenance uncertain): UPNG 515, adult male, 28 June 1970, skull and skeleton.

Milne Bay Province

8. Biniguni, 150 m (09°41′S 149°17′E): AMNH 157129, adult male, 31 August 1953, trophy mandible.
9. Peria Creek, 2 mi northeast of Opaigwari, 50 m (09°42′S, 149°23′E): AMHN 157130, adult male, 20 August 1953, skin and skull; AMHN 157131, adult male, 31 August 1953, skin and skull; AMNH 157132, subadult male, 1 September 1953, skin and skull; AMNH 157133, adult female, 1 September 1953, skin and skull, with two accompanying female pouch young in alcohol (labeled AMNH 158982 and 152983); AMNH 157134, adult male, 5 September 1953, skin and skull; and AMNH 157135, subadult female, 5 September 1953, skin and skull.
10. Cape Vogel Peninsula, 2 mi north of Menapi (09°46′S, 149°58′E): AMNH 157128, adult male, 24 April 1953, mandible.

Oro (= Northern) Province

11. Ioma, Mambare River (08°22′S, 147°48′E): BMNH 6.10.8.21, juvenile male, 8 May 1906, skin only, collected by C.A.W. Monckton.
12. Amboga, near Popondetta, 200 ft (08°42′S 148°13′E): BBM-NG 29932, adult female, 10 October 1963, skin and skull; BBM-NG 29930, juvenile male, 10 October 1963, skin (apparently young of BBM-NG 29932).

The 10 specimens from Central Province all lack precise elevational data. However, at least three of the five localities (Goldie River, Sogeri Plateau, and the Maguli Range) are situated in the foothills of the Owen Stanley Range at 400–600 m or higher. We have examined the AMNH specimens previously referred to *broadbenti* by Tate and Archbold (1937: 353) and Tate (1948b: 327) from the Central Province localities of Sogeri (450 m), Mafulu (1250 m), Kagi (1500 m), and Murray Pass (2860 m). These specimens actually represent *Peroryctes raffrayana,* as anticipated by George and Maynes (1990: 95) and Flannery (1995: 118). Importantly, these and other vouchered specimens of *P. raffrayana* from the Owen Stanleys, especially specimens from the Goldie River (BMNH), Sogeri Plateau (AMNH), and Kagi (AMNH, adjacent to the Maguli Range) confirm the elevational overlap and local co-occurrence of *Peroryctes broadbenti* and *P. raffrayana* in the Kokoda area (cf. Ziegler, 1977).

The 10 specimens from Milne Bay Province were all obtained during the Fourth Archbold Expedition to Collingwood Bay in 1953 (Brass, 1956).

The three specimens from Oro (= Northern) Province come from localities about 50 km apart. The adult female (BBM-NG 29932) and juvenile male (BBM-NG 29935) collected near Popondetta in 1963 have the same collection details, and presumably represent a mother-offspring pair. A juvenile male skin (BMNH 6.10.8.21) collected at Ioma in 1906 was referred to *P. broadbenti* by Flannery (1995: 118) on the basis of pelage coloration, and we confirm this identification based on our own examinations. One additional record of *P. broadbenti* from Oro Province is a recently collected ear clip sample from Ajoa River, Tufi District (09°20′S, 148°55′E). The identity of this otherwise nonvouchered bandicoot was confirmed by comparison of mitochondrial DNA from this animal with DNA extracted from the holotype of *P. broadbenti* (Westerman and Aplin, in prep.).

Available records for *P. broadbenti* cluster in three widely separated geographic areas situated both north and south of the central cordillera of the southeastern peninsula of Papua New Guinea. Whether this represents a truly fragmented geographic distribution or simply results from inadequate collecting in the intervening country is an important question that we cannot answer with certainty. However, it is perhaps not surprising that two of the three regions (the hinterlands of Port Moresby and Collingwood Bay) are among the most intensively sampled areas on the New Guinea mainland (e.g., see Flannery, 1995: 64, map 11). In contrast, much of the lowland and foothill country around the southeastern peninsula has received little zoological attention, despite its proximity to some large population centers.

The few specimens of *P. broadbenti* with precise elevational data all come from between 50–150 m on the north side of the peninsula. However, as noted above, some of the specimens from the foothills of the Owen Stanley Range probably derive from higher elevations, perhaps up to 500 or even 1000 m.

External Morphology of *P. broadbenti*

Ramsay's (1879) account of *P. broadbenti* included a detailed description of the external morphology and was accompanied by excellent illustrations rendered by Baron Miklouho-Maclay; several of these are reproduced here (fig. 3). A color plate of the mounted holotype is contained in Flannery (1995), along with a photograph of a living animal (possibly PNGNM 23714). The following account of the morphology of *P. broadbenti* is based primarily on the holotype and the AMNH series from Peria Creek, Milne Bay Province. External measurements and weights of individual specimens are given in table 1.

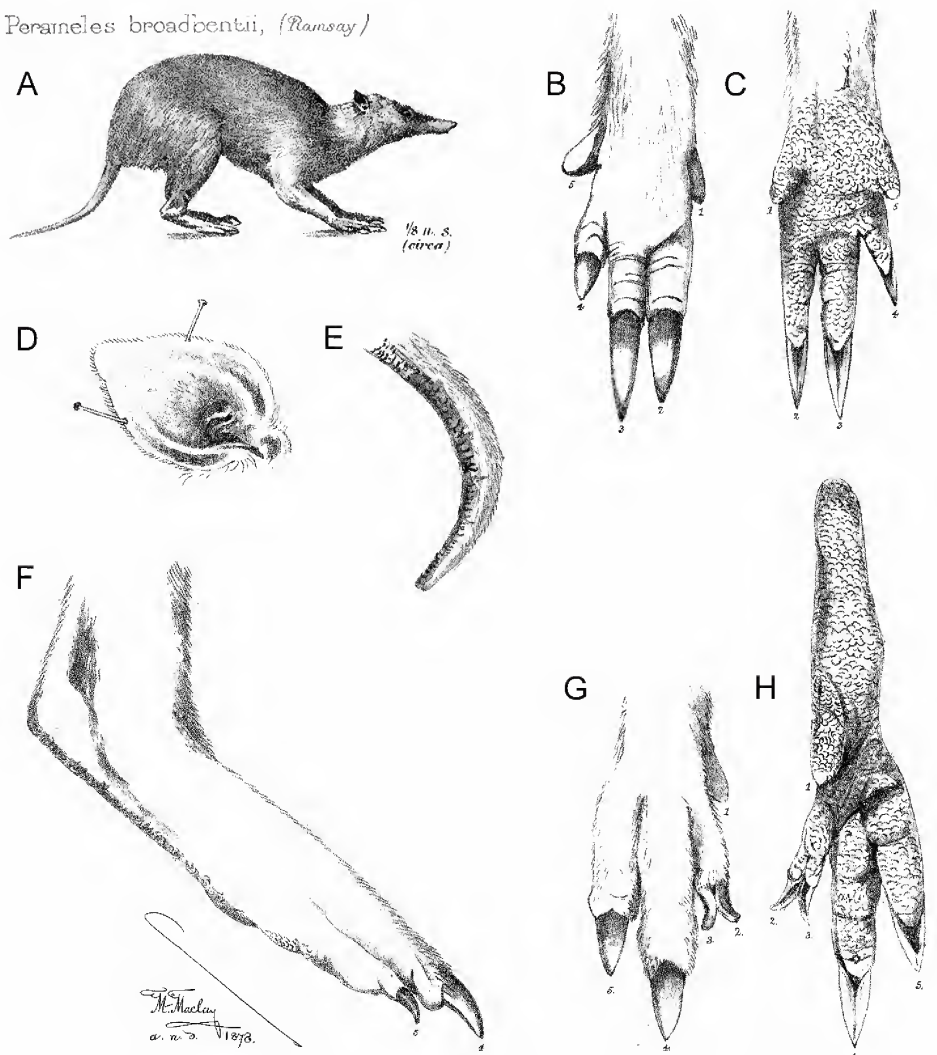

FIGURE 3. Illustrations of the holotype of *Peroryctes broadbenti* by Baron Miklouho-Maclay, originally published by Ramsay (1879) and reproduced here with permission of the Linnean Society of New South Wales. **A.** View of entire body, in profile. **B.** Dorsal view of right manus. **C.** Ventral view of right manus. **D.** Lateral view of right pinna. **E.** Close-up view of the terminal portion of the tail. **F.** Lateral view of right pes. **G.** Dorsal view of digits of right pes. **H.** Ventral view of right pes.

TABLE 1. External measurements of individual specimens of *P. broadbenti,* with summary metrics for each sex. Values in square brackets are calculated by subtraction from other measurements. Measurements qualified with an asterisk (*) were taken from a puppet skin; u = unknown sex. Specimen numbers qualified with an asterisk are juvenile or young adult individuals and their measurements are not included in the summary statistics. Values for AM A3238 are converted from imperial measurements given by Ramsay (1879).

Specimen	Sex	Province	Weight (kg)	Total Length	Head + Body	Tail	Pes	Ear
AM A3238	♂	CP	—	709	508	[195]	99	—
AMNH 222624	♂	CP	>4	—	480	190	98	25
NMW 109	♂	CP	—	—	—	—	—	—
PNGNM 23390	♂	CP	—	—	—	—	—	—
PNGNM 23726*	♂	CP	—	—	—	—	—	—
UPNG 515*	♂	CP	>3	—	435	95	87	29
UPNG 557	♂	CP	4.9	—	558	95	87	29
PNGNM 23714	♀	CP	—	—	—	153*	76*	30*
PNGNM 23727*	♀	CP	—	—	—	—	—	—
PNGNM 24028	♀	CP	—	—	—	—	—	—
AMHN 157130	♂	MBP	4.76	787	[558]	229	100	42
AMHN 157131	♂	MBP	3.8	751	[525]	220	96	42
AMNH 157134	♂	MBP	2.88	695	[480]	215	83	42
AMNH 157133	♀	MBP	1.42	567	[394]	173	77	39
AMNH 157135	♀	MBP	0.938	460	[340]	120	69	36
BMNH 6.10.8.21	♂	OP	—	—	—	—	—	—
BBM-NG 29932	♀	OP	—	551	[395]	156	79	37
BBM-NG 29930*	♂	OP	—	308	[222]	86	58	30

The few available body weights for *P. broadbenti* indicate a striking level of sexual dimorphism, with males attaining body weights to 4.9 kg (n = 5), more than three times the weight of females (to 1.4 kg; n = 2). (An entry in *Encyclopaedia Britannica* [2010] states that *P. broadbenti* can weigh up to 7 kg; while this may well be true, as far as we know there is no evidence to support this claim.) This dimorphism is mirrored in head-body lengths (<400 mm in females, >400 mm in males) and hindfoot lengths (<80 mm in females, >80 mm in males), which likewise distinguish adult males and adult females, at least in the small samples available. Ear length does not differ between the sexes, but the few available adult measurements point to a possible difference in ear length between animals from Central Province (25–30 mm; n = 4) and those from Oro and Milne Bay provinces (36–42 mm; n = 6). While we assume that all accompanying ear measurements represent the greatest length from the notch to the distal margin of the pinna, we are not certain. Measurements from additional specimens are needed to confirm whether these apparent geographic differences in ear length represent true dimensional distinctions or simply different techniques of measurement.

The dorsal pelage is a uniform reddish-brown flecked with black due to the presence of abundant stiff, black guard hairs. The overall texture is coarse but not spiny. The flanks are a brighter reddish brown, grading evenly into a broad, fawn to pale orange venter. Contrary to a statement by Menzies (1991), the venter never shows patches of pure white fur (any such individuals represent examples of *P. raffrayana*; see below). The face is thinly clothed with short gray-brown fur (Ramsay suggests "an ashy tint pencilled with black hairs" [1879: 403]) and the muzzle is sparsely furred. The external ears are elongate and relatively narrow; their lower

border contains a weakly developed bursa. Ramsay (1879: 403) mentions "in the hollow of the ear are two transversely naked parallel folds with a narrow deep fissure between them" (these folds are no longer visible on the dried specimen). The ears of the type now appear uniformly dark but Ramsay's (1879: 403) account indicates that they were "blackish without, light fawn-color within, almost naked, sparingly clothed with minute fawn-colored hairs." The snout was described as "naked and parallel longitudinal lines at the tip; the median fissure distinct." The figure of the rhinarium shows vertically oriented striae.

The manus and pes are thinly clothed in pale fawn hairs, the manus so sparingly as to appear almost naked. The plantar surface of the manus and pes is coarsely and evenly granular. Although Ramsay's figure of the pes shows deep folding of the plantar skin (fig. 3), there is no suggestion of discrete plantar pads of the kind seen in some other New Guinean bandicoots (e.g., *Echymipera rufescens* and *E. davidi* Flannery, 1990b). The tarsal and metatarsal portion of the pes, measured along the central toe, is approximately equal in length to the phalangeal portion.

The tail measures approximately one-third of the combined length of the head and body, though apparently differs in length according to sex (see above). The tail is scaly and thinly furred above and more coarsely scaled and unfurred below. Ramsay (1879: 403) reported that the tail of the holotype was "blackish above for about two-thirds of its length, from thence fawn-color to the tip, sparingly clothed with short hair."

Female *P. broadbenti* have four pairs of teats within a distinct pouch that opens to the rear (e.g., AMNH 157133, 157135). The scrotum of males is sparsely furred and concolorous with the venter.

Craniodental Morphology of *P. broadbenti*

The cranium and dentary of the holotype of *P. broadbenti* are illustrated in figure 4 alongside an adult male (AMNH 157134) from the north coastal Peria Creek population. The overall morphological similarity of the two populations is evident both from the illustrations and from comparison of cranial and dental measurements (see table 2). However, certain differences are also apparent, most notably the holotype has a broader anterior palate and shallower rostrum, a narrower postorbital constriction, more flared posterior zygomatic roots, more elongate orbitotemporal fossae, and a broader ascending ramus of the dentary. The minimum width across the postorbital constriction appears to consistently distinguish male specimens from the two areas, with ranges of 13.7–14.3 mm (n = 3) for males from Central Province, compared with 14.6–15.1 (n = 4) for specimens from Peria Creek in Milne Bay Province. Another notable difference between the two figured specimens concerns the size of the upper and lower third premolars—these are considerably larger in AMNH 157134 than in the holotype. However, other male specimens from Peria Creek show a wide variation in third premolar length (table 2), including individuals with third premolars slightly shorter than those of the holotype.

The marked sexual dimorphism in craniodental morphology in this species is illustrated by comparison of similar-aged male and female specimens from the Peria Creek population (fig. 5). The male cranium is not only larger than that of females but also differs somewhat in

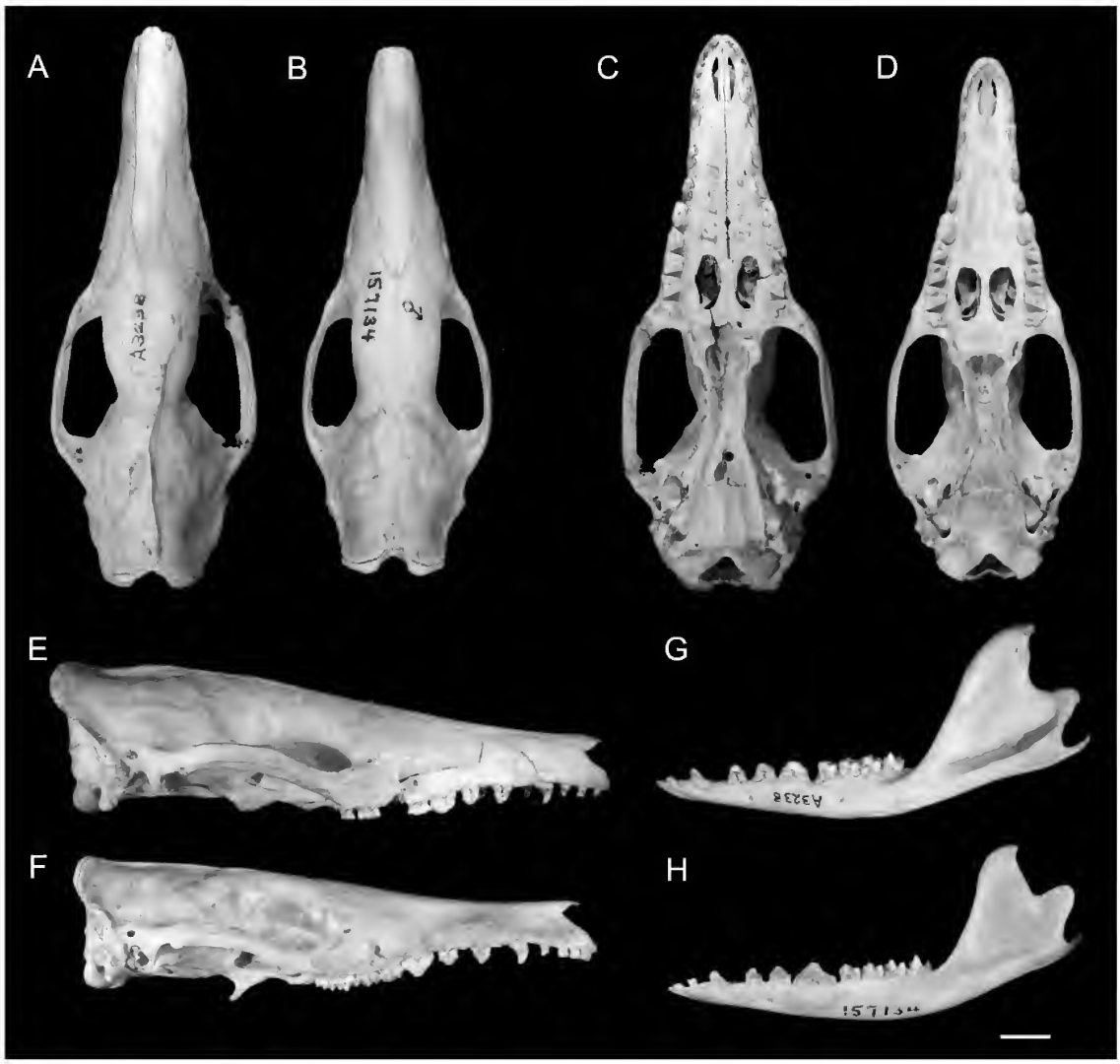

FIGURE 4. Interpopulational cranial variability in male *P. broadbenti.* Dorsal, ventral, and lateral views of the cranium and lateral views of the dentary in two adult male specimens of *Peroryctes broadbenti*: **A, C, E, G.** The holotype, AM A3238, from inland of Port Moresby, Central Province; **B, D, F, H.** AMNH 157134, from Peria Creek, Milne Bay Province. Scale bar = 10 mm.

shape, due mainly to a proportionally more elongate rostrum in males. Somewhat surprisingly, given the size contrast, there is little if any difference in the general robustness of the cranium between the sexes. In *P. broadbenti,* individuals of both sexes progressively develop heavier zygomatic arches and more prominent temporal and nuchal ridges with age, with no obvious difference in degree between the sexes. One other possible difference concerns the size of the posterior palatine foramina, which show no overlap in lengths between the sexes (table 2). However, measurements from more specimens are needed to assess consistency in this feature.

TABLE 2. Cranial and dental measurements for individual adult specimens of *P. broadbenti*.

	AM A3238	AMNH 157130	AMNH 157131	AMNH 157134	AMNH 222624	PNGNM 23390	NMW 109	UPNG 557	UPNG 515	AMNH 157133	BBM-NG 29932	PNGNM 24028
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀
bcl	110.5	109.5	106.2	101.4	107.0	115.3	—	108.2	102.3	84.8	84.3	91.2
onl	117.0	114.8	114.2	104.6	113.0	120.8	116.0	114.6	107.1	88.4	85.3	95.1
bol	19.9	19.0	19.0	17.3	19.1	—	—	—	—	14.3	15.0	—
bsl	17.8	17.9	17.1	16.3	17.5	—	—	—	—	12.4	12.0	—
mw	30.9	31.7	30.9	27.8	30.9	27.3	—	—	—	24.6	25.5	24.6
zw	—	42.9	42.6	37.6	44.1	—	—	42.7	39.5	32.8	33.7	35.6
cw	21.1	22.4	20.6	20.0	20.1	—	—	—	—	17.7	17.9	—
POW	23.7	26.1	23.3	22.6	23.1	—	—	—	—	19.4	19.2	—
oM4	24.6	24.4	24.3	22.8	24.8	—	—	—	—	20.7	21.0	—
oP3	21.3	21.4	20.9	19.0	19.5	—	—	—	—	16.3	15.6	—
apl	9.7	7.7	7.8	7.6	8.8	—	—	—	—	6.6	6.1	—
apw	4.7	4.3	4.2	3.8	4.6	—	—	—	—	3.6	3.2	—
ppl	11.6	11.6	10.3	10.7	10.8	—	—	—	—	8.2	8.2	—
rwi	19.8	19.3	18.8	17.5	18.9	—	—	—	—	15.8	14.9	—
rwc	12.8	13.1	12.0	11.3	13.3	—	—	—	—	10.0	9.3	—
nl	51.5	47.2	47.7	45.4	46.8	—	46.5	49.8	47.8	38.3	37.5	—
anw	6.7	6.3	6.4	5.5	5.5	—	—	—	—	4.4	4.3	—
pnw	6.9	7.2	7.2	6.2	7.3	—	—	—	—	5.5	5.6	—
nps	21.9	23.5	21.5	19.0	19.4	—	—	—	—	16.5	15.7	—
fs	30.8	29.0	27.9	26.7	28.6	—	—	—	—	25.1	21.7	—
iow	13.7	14.6	15.1	14.9	14.1	14.1	—	—	—	13.8	14.0	14.3
ppw	19.2	17.8	17.1	17.0	19.3	—	—	—	—	15.5	15.9	—
aIL	8.6	8.8	8.5	8.1	8.2	—	—	—	—	7.5	7.6	—
IL	12.6	12.4	11.5	11.5	12.1	—	—	—	—	10.3	10.4	—
ctl	36.6	35.0	34.6	33.6	33.8	—	—	—	—	28.7	34.3	—
uMR	17.3	16.9	16.4	16.7	17.4	—	—	—	—	15.9	15.3	—
uML	14.5	14.7	13.8	14.2	14.6	—	—	—	—	13.7	13.6	—
P1L	3.3	3.3	3.2	3.2	4.1	—	—	—	—	2.7	3.4	—
P1W	1.4	1.5	1.2	1.4	1.3	—	—	—	—	1.0	1.1	—
P2L	4.0	3.8	3.9	3.8	3.9	—	—	—	—	3.4	3.7	—
P2W	1.7	2.0	1.8	1.7	1.7	—	—	—	—	1.6	1.4	—
P3L	5.5	6.4	6.4	6.7	5.4	—	—	—	—	3.5	3.6	—
P3W	3.3	4.3	4.1	3.7	3.7	—	—	—	—	2.0	1.7	—
lmr	17.6	18.0	17.7	18.1	18.3	—	—	—	—	17.2	16.0	—
lpr	17.5	19.0	18.1	17.7	17.9	—	—	—	—	14.5	13.8	—
p1L	3.3	3.5	3.1	3.3	4.1	—	—	—	—	2.8	3.2	—
p2L	3.9	4.4	4.3	4.2	4.5	—	—	—	—	3.9	3.9	—
p3L	5.9	7.2	8.1	8.1	6.3	—	—	—	—	4.9	4.8	—

Within the dentition, the most striking sexual dimorphism is observed in the premolar row (fig. 6; table 2). In females, the three premolars in each of the upper and lower series form an evenly graded series with similar size increments from P1 to P2 and from P2 to P3. In contrast, males possess massively hypertrophied upper and lower third premolars that are much longer and also wider than the corresponding P2. Apart from this considerable size difference, the P3s do not differ in morphology between the sexes. The molar series is slightly

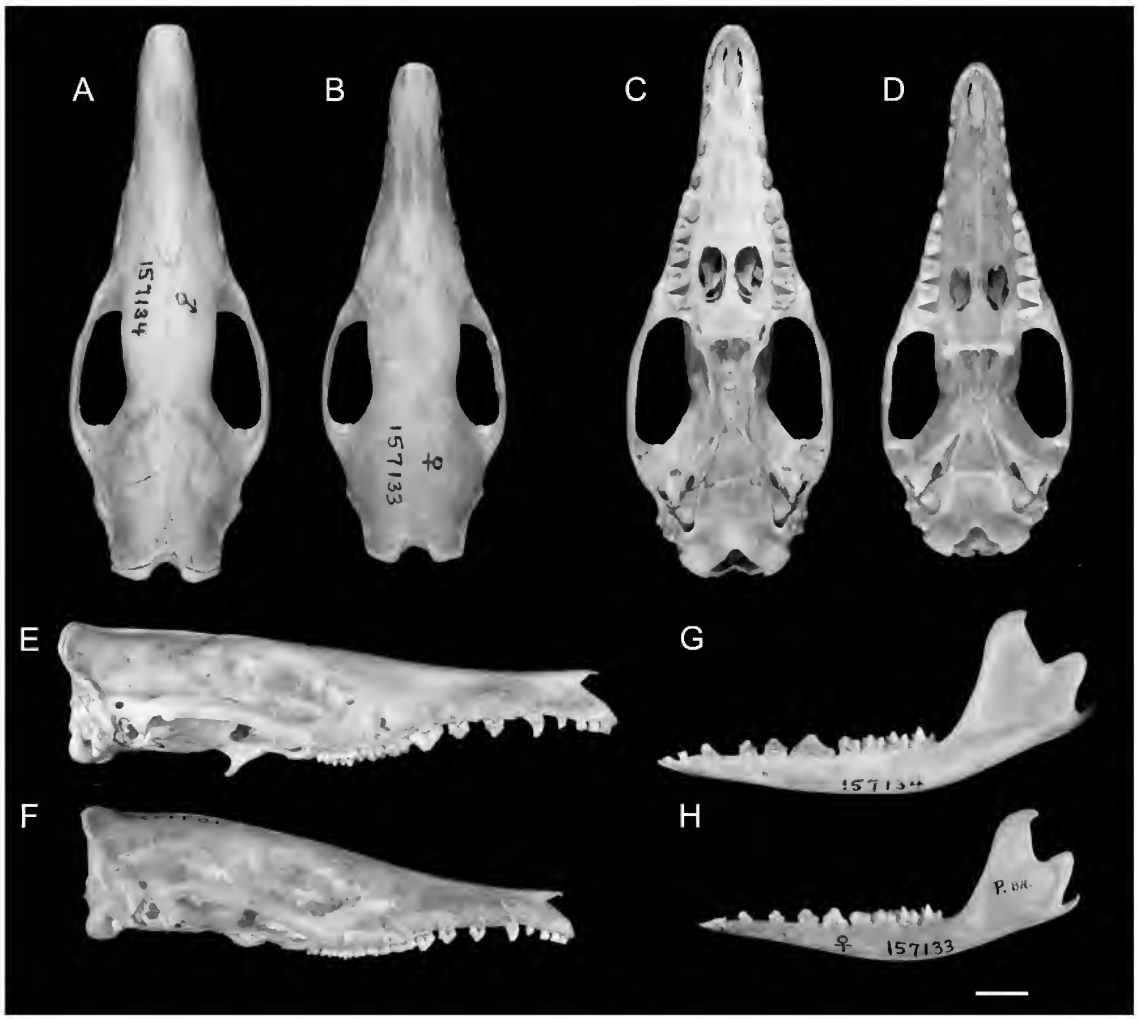

FIGURE 5. Intrapopulational sexual dimorphism in cranial morphology in *P. broadbenti*. Dorsal, ventral, and lateral views of the cranium and lateral views of the dentary in adult male and female specimens of *Peroryctes broadbenti* (from Peria Creek, Milne Bay Province): **A, C, E, G.** AMNH 157134, adult male; **B, D, F, H.** AMNH 157133, adult female. Scale bar = 10 mm.

more elongate in males than females, with no observed overlap between the small samples of each sex (table 2).

The upper and lower canines of *P. broadbenti* are relatively small in both sexes (fig. 6). Canine size in bandicoots is difficult to quantify due to heavy wear of the crowns and continued growth of the roots. Nevertheless, it is clear that sexual dimorphism in canine size, a feature observed in some other bandicoots (see Discussion), is weakly developed or absent in *P. broadbenti*.

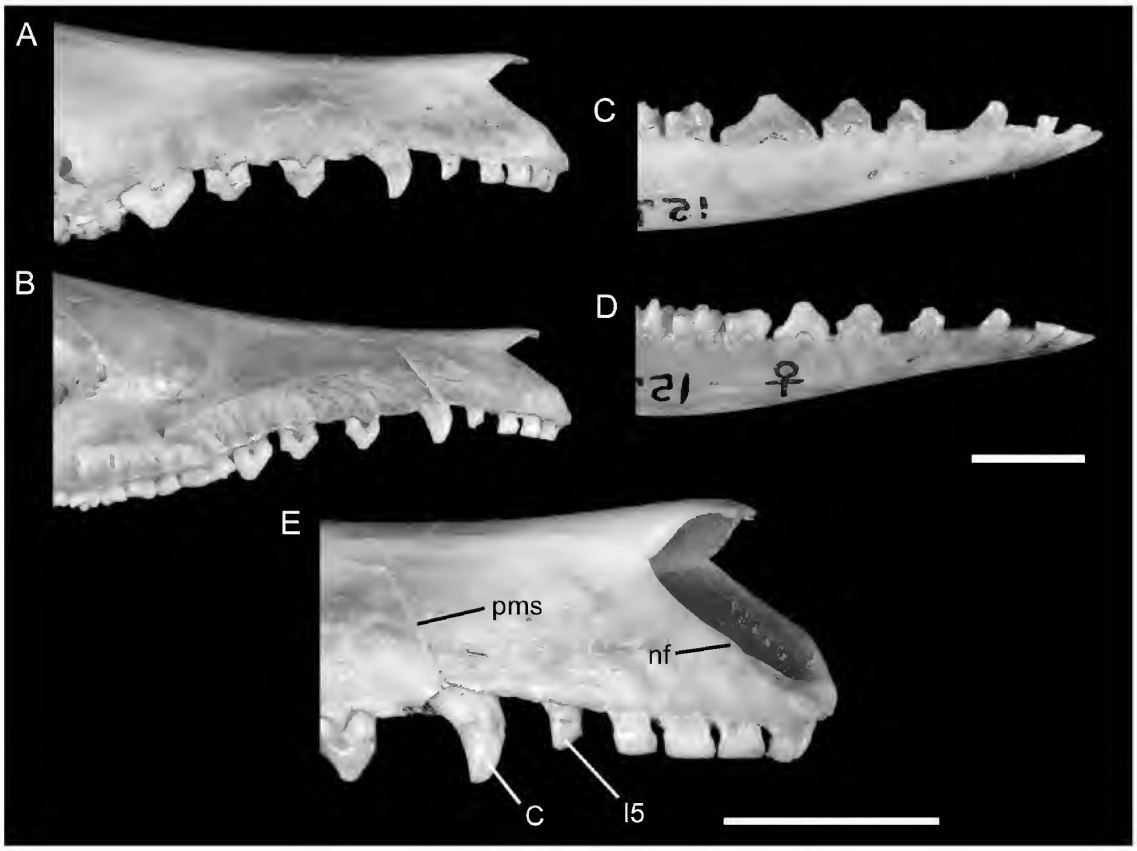

FIGURE 6. Morphology of the rostrum and anterior dentition in *Peroryctes broadbenti.* Views of upper and lower anterior dentitions (incisors, canine, and premolars) of adult male and female specimens of *Peroryctes broadbenti* (from Peria Creek, Milne Bay Province). Lateral views: **A, C.** AMNH 157134, adult male; **B, D.** AMNH 157133, adult female. Scale bar = 10 mm. Close-up anterolateral view: **E.** AMNH 157134, adult male, showing placement of the canine (labelled C, behind I5) on the premaxillary-maxillary suture, and the lack of winglike processes on the narial flange of the premaxillae (compare with the configuration of *Microperoryctes ornata,* fig. 12). Scale bar = 10 mm. Abbreviations: **pms,** premaxilla-maxilla suture; **nf,** narial flange of premaxilla.

Comparison with *P. raffrayana* and Other New Guinean Bandicoots

Samples of *Peroryctes broadbenti* and *P. raffrayana* from southeastern New Guinea are readily distinguishable on the basis of pelage color. As noted earlier, the dorsal pelage of *P. broadbenti* is a rather uniform reddish brown, grizzled with dark blackish-brown flecks. In contrast, the dorsal pelage of *P. raffrayana* is a darker reddish brown with a subtle increase in reddish suffusion toward the rump. The flanks in *P. broadbenti* are a rich reddish brown, contrasting with the duller hues of the dorsum, whereas in *P. raffrayana* the pelage on the flanks is not differentiated from that on the dorsum. The ventral pelage also differs markedly between the two species. In *P. broadbenti* the venter is a uniform pale orange or fawn color, without any trace of encroachment from the darker-colored sides. In *P. raffrayana* the venter is a boldly patterned mosaic of dark reddish-brown fur, a continuation of the flanks, interspersed with patches

of pure creamy white fur that are most extensive anteriorly, covering the chin, throat, and pectoral region, and posteriorly, centered on the inguinal region. In some specimens, these patches are linked by a thin midventral band of cream fur. However, in others, the darker fur of the sides meets across the midventer and disrupts this midventral connection. In such cases, the creamy white fur on the throat typically is also narrowed to a thin stripe extending toward the chin.

The dorsal surfaces of the manus and pes also differ markedly between the two species. These are thinly furred and very pale brown in *P. broadbenti* but densely furred and dark reddish brown in *P. raffrayana.*

Species of other bandicoot genera are readily distinguished from *P. broadbenti* by a combination of pelage texture and coloration. Species of *Echymipera* and *Isoodon* have more densely spinous pelage (Flannery, 1995) while regionally sympatric species of *Microperoryctes* are softer furred and more brightly patterned, with a dark middorsal stripe and dark bars on the rump (Aplin and Woolley, 1993; Helgen and Flannery, 2004).

Craniodental Morphology

The cranium and dentary of adult male individuals of *P. broadbenti* and *P. raffrayana* are compared in general views in figure 7; more detailed comparisons of cranial and dental morphology in *P. broadbenti* and *P. raffrayana* are shown in figures 8–10. We note the following key cranial differences between the two species:

1. Anterior part of rostrum is relatively broader in *P. broadbenti* (fig. 7);
2. Upper molar rows are less divergent posteriorly in *P. broadbenti* (fig. 7);
3. Posterior palatal foramen on each side terminates slightly further posteriorly in *P. broadbenti* (just forward of M2) than *P. raffrayana* (anterior edge of M1) (fig. 7);
4. Incisive foramen on each side terminates further anteriorly in *P. broadbenti* (level with I5) than *P. raffrayana* (midway between I5 and C) (fig. 7);
5. Interorbital region relatively narrower in *P. broadbenti* (fig. 7);
6. Auditory bullae relatively smaller in *P. broadbenti* (figs. 7, 8);
7. Hamular process of each pterygoid bone is shorter and deeper in *P. broadbenti* (figs. 7, 8);
8. Foramen rotundum with more elongate lateral bony tube in *P. broadbenti* (fig. 8);
9. Paroccipital processes more elongate in *P. broadbenti* (fig. 9);
10. Sagittal and nuchal crests more strongly produced in *P. broadbenti,* hence occipital surface of cranium is much deeper for its width (fig. 9);
11. Exoccipital and supraoccipital bones show differing sutural relations around foramen magnum in *P. broadbenti* (with left and right exoccipital bones in medial contact, excluding supraoccipital from foramen magnum) and *P. raffrayana* (exoccipital bones widely separated, supraoccipital forms superior margin of foramen magnum) (fig. 9);
12. Coronoid process of dentary relatively taller in *P. broadbenti* (fig. 7);
13. Angular process of dentary longer in *P. broadbenti* (terminating well behind articular condyle; terminating just behind condyle in *P. raffrayana*) (fig. 7);
14. Upper incisor series in *P. broadbenti* shows only slight increase in length from I1 to I4 (I4 is much longer than I1 in *P. raffrayana*) (fig. 7);

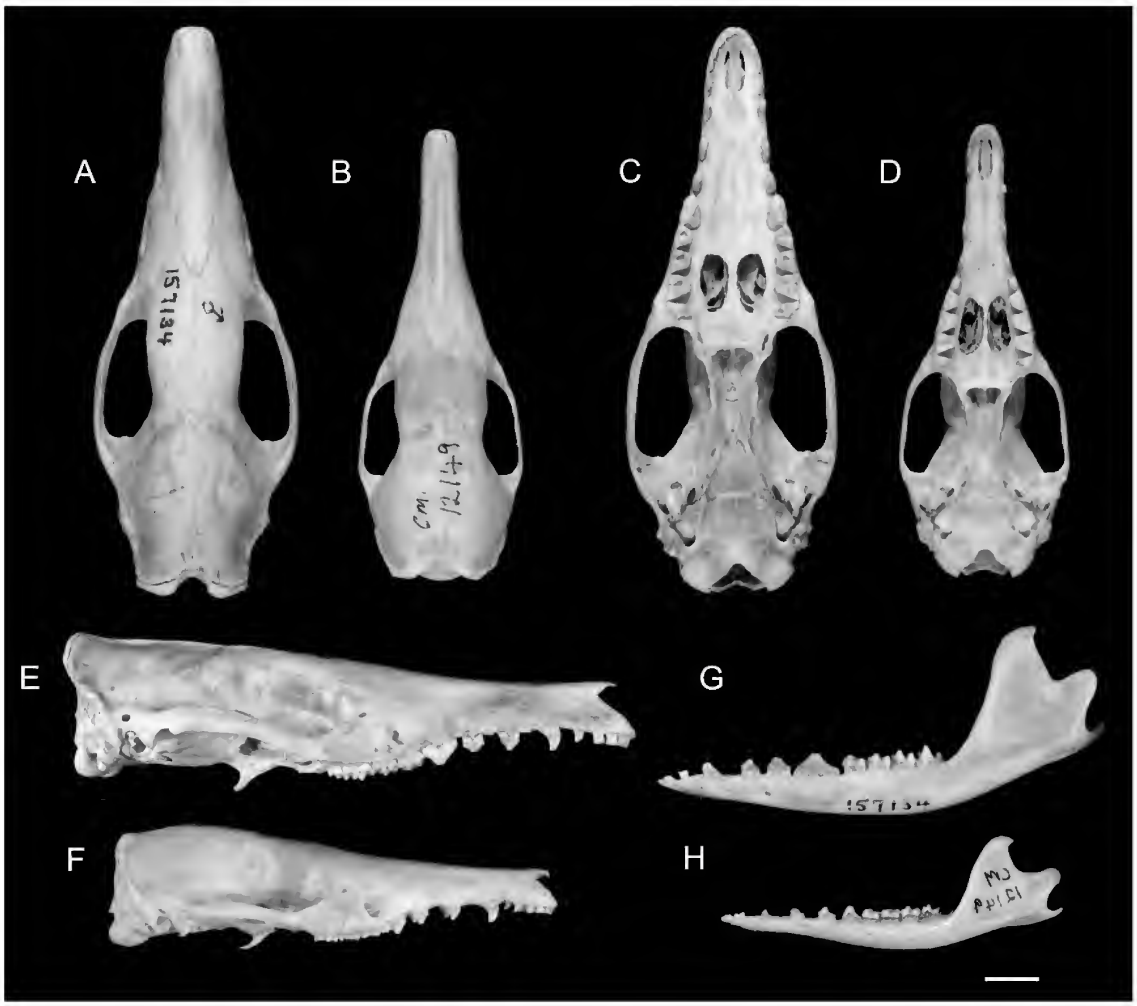

FIGURE 7. Interspecific cranial variability in *Peroryctes*. Views of the cranium and dentary of adult male specimens of the two species of *Peroryctes*: **A, C, E, G.** AMNH 157134, *P. broadbenti* from Peria Creek, Milne Bay Province; **B, D, F, H.** CSIRO M8607, *P. raffrayana* from Uinba, Wahgi Valley, Western Highlands Province. Scale bar = 10 mm.

15. P3 in *P. broadbenti* lacks a distinct posterolingual cingulum (present in *P. raffrayana*) (fig. 10);
16. All upper and lower premolars slightly larger relative to molar size in *P. broadbenti* (fig. 7; table 5);
17. Upper and lower third premolars in male specimens of *P. broadbenti* much longer and higher crowned than preceding tooth (last two premolars are approximately equal lengths in *P. raffrayana*) (fig. 7; table 5);
18. Anterior cingulum transversely continuous on M1–3 in *P. broadbenti* (only complete on M1, interrupted on M2–3 in *P. raffrayana*) (fig. 10);

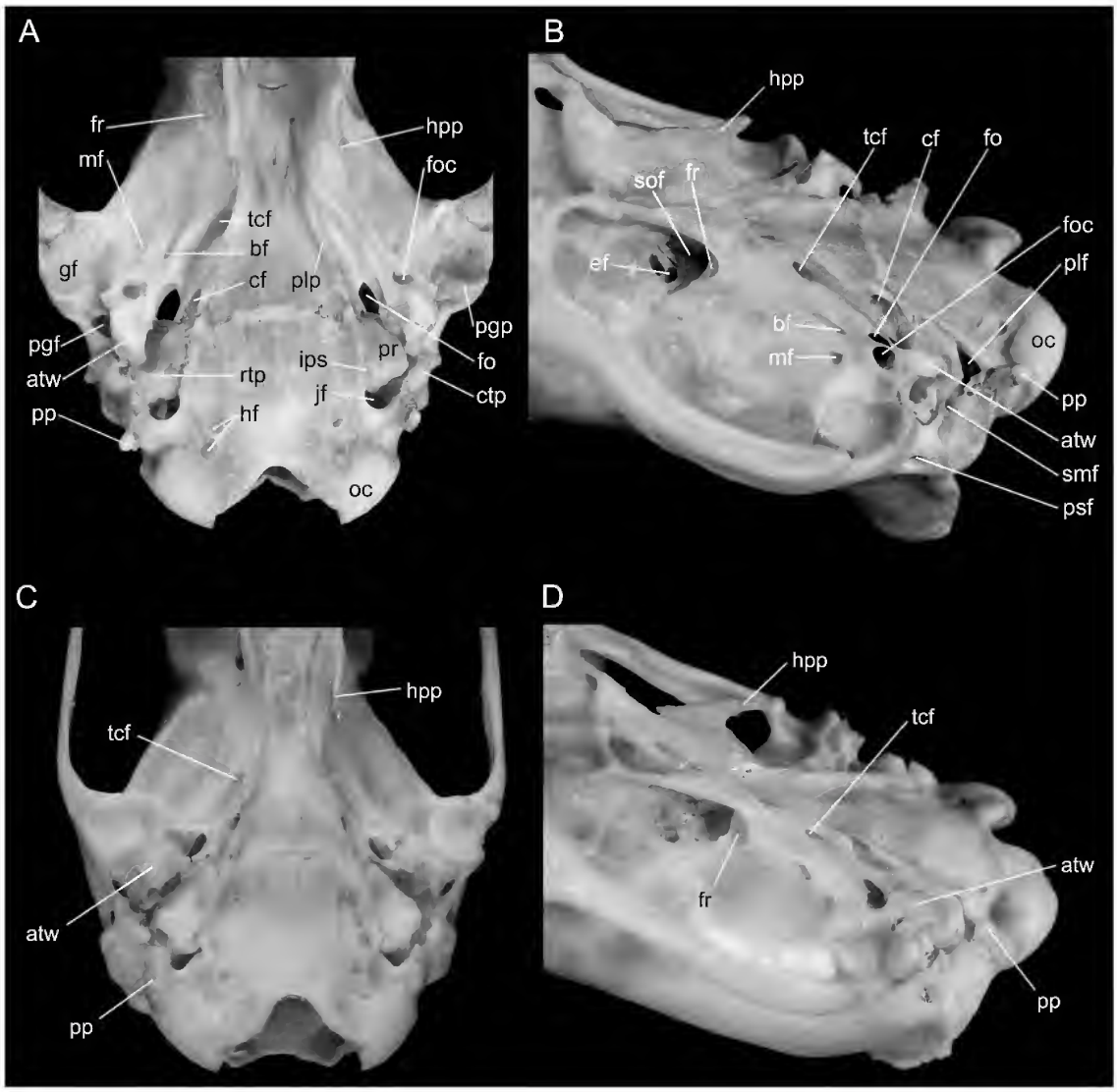

FIGURE 8. Views of the basicranial region of the two species of *Peroryctes,* showing general anatomy and characteristic contrasts between the two species: **A.** AMNH 157134, *P. broadbenti,* adult male; **B.** CSIRO M8607, *P. raffrayana,* adult male. Abbreviations: **atw,** alisphenoid tympanic wing; **bf,** foramen for buccinator nerve; **cf,** carotid foramen; **ctp,** caudal tympanic process; **ef,** ethmoidal foramen; **fo,** foramen ovale; **foc,** lateral opening of foramen ovale canal; **fr,** foramen rotundum; **gf,** glenoid fossa; **hf,** hypoglossal foramina; **hpp,** hamular process of pterygoid; **ips,** foramen for inferior petrosal sinus; **jf,** jugular foramen; **mf,** foramen for masseteric nerve; **oc,** occipital condyle; **pgf,** postglenoid fossa; **pgp,** postglenoid process; **plf,** posterior lacerate foramen; **plp,** posterior lamina of pterygoid; **pp,** paroccipital process; **pr,** promontorium of petrosal; **psf,** postsquamosal foramen; **rtp,** rostral tympanic process; **smf,** stylomastoid foramen; **sof,** sphenorbital fissure; **tcf,** foramen for transverse sinus canal.

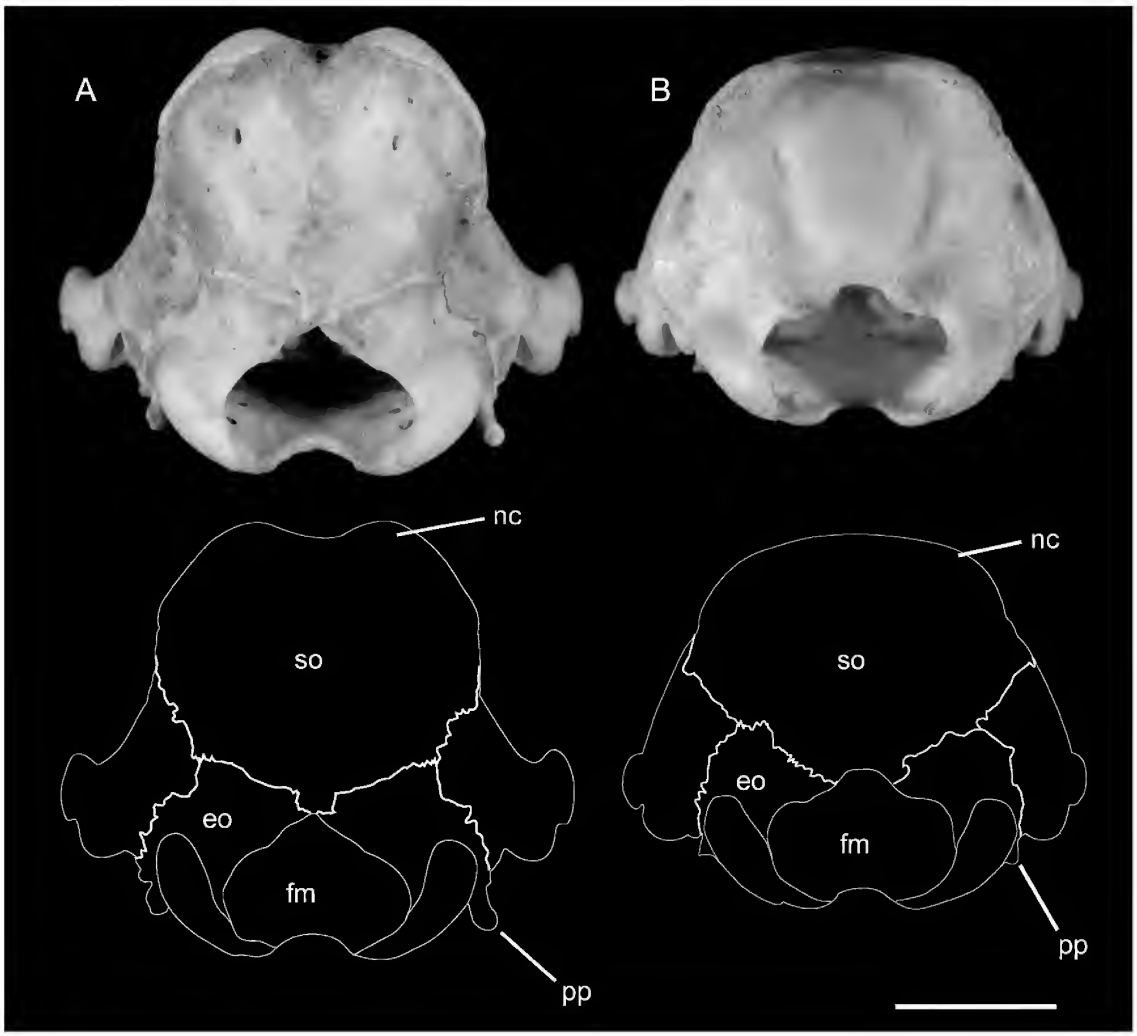

FIGURE 9. Posterior surface of the cranium in the two species of *Peroryctes*: **A.** AMNH 157134, *P. broadbenti,* adult male; **B.** CSIRO M8607, *P. raffrayana,* adult male. In this view, differences can be seen in the shape of the occiput, especially with respect to the development of the nuchal crest; the course of the suture between the incompletely fused exoccipital and supraoccipital bones, especially with respect to the sutural termination at the foramen magnum (emphasized in the line drawings below each skull); and the development of the paroccipital processes. Scale bar = 10 mm. Abbreviations: **so,** supraoccipital bone; **eo,** exoccipital bone; **fm,** foramen magnum; **nc,** nuchal crest; **pp,** paroccipital process.

19. Stylar shelf in *P. broadbenti* in M1–3 is incompletely breached between the centrocrista and ectoflexus (breach is complete in *P. raffrayana* but remnants of centrocrista retained as enamel "spurs" on M1–2, absent on M3) (fig. 10);
20. Stylar cusp C smaller than stylar cusp D on M3 (subequal in size on M3 of *P. raffrayana*) (fig. 10);
21. Metacone of M4 more prominent in *P. broadbenti* (fig. 10);

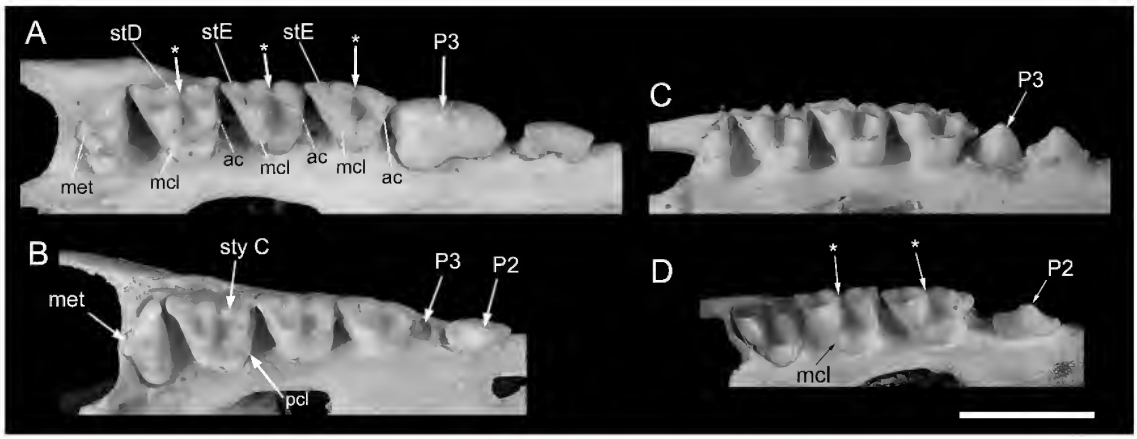

FIGURE 10. Views of the right upper molar series of the two species of *Peroryctes*: **A.** AMNH 157134, *P. broadbenti,* male with P3 and M1–4 fully erupted; **B.** AMNH 157132, *P. broadbenti,* male with P3 in crypt and M4 partly erupted; **C.** AM M13705, *P. raffrayana* (Kobobip, West Sepik Province), male with P3 partly erupted and M1–4 fully erupted; **D.** CSIRO M12250, *P. raffrayana* (Opanabu, Milne Bay Province), male with P3 and M4 unerupted, and M3 in crypt. Scale bar = 5 mm. Abbreviations and denotations: **ac,** anterior cingulum; **mcl,** metaconule; **met,** metacone; **pcl,** protoconule; **stC,** stylar cusp C; **stD,** stylar cusp D; **stE,** stylar cusp E; * = remnants of centrocrista. Premolar homologies are denoted.

22. m1–3 are relatively broader and have proportionally shorter talonids in *P. broadbenti* (fig. 11);
23. Paraconids of m1–3 are more elevated in *P. broadbenti* (most notable on m1, less so on posterior molars) (fig. 11);
24. Cristid obliqua of m1–3 is more lingually inflected in *P. broadbenti* (meets rear of trigonid lingual to metacristid notch vs. labial to notch in *P. raffrayana*) (fig. 11);
25. Trigonid of m1 is broader, more bulbous in *P. broadbenti* (fig. 11);
26. Anterior cingulum of m2 is narrower in *P. broadbenti* (fig. 11);
27. Entoconids of m1–3 in *P. broadbenti* are broader, with shorter preentocristids (almost absent on m3) that do not contact the rear of the trigonids (entoconids more bladelike in *P. raffrayana,* with elongate preentocristids and commonly with a slight "metastylid" on m1 or m1–2) (fig. 11);
28. m4 is relatively more elongate in *P. broadbenti,* reflecting elongation of anterior cingulum and lengthening of talonid (fig. 11).

Despite this extensive list of differences between *P. broadbenti* and *P. raffrayana,* these taxa together are distinguished from all other New Guinean bandicoots by a similarly impressive suite of craniodental features. Some of these features are enumerated below as a starting point for a generic definition of *Peroryctes.* The condition of certain features in *Microperoryctes ornata* is illustrated in figure 12 for comparison. Features noted previously by Groves and Flannery (1990; table 2b) are indicated below by a "G&F" code. Other features listed by Groves and Flannery (1990) generally are not as consistent as claimed; these will be reviewed in a

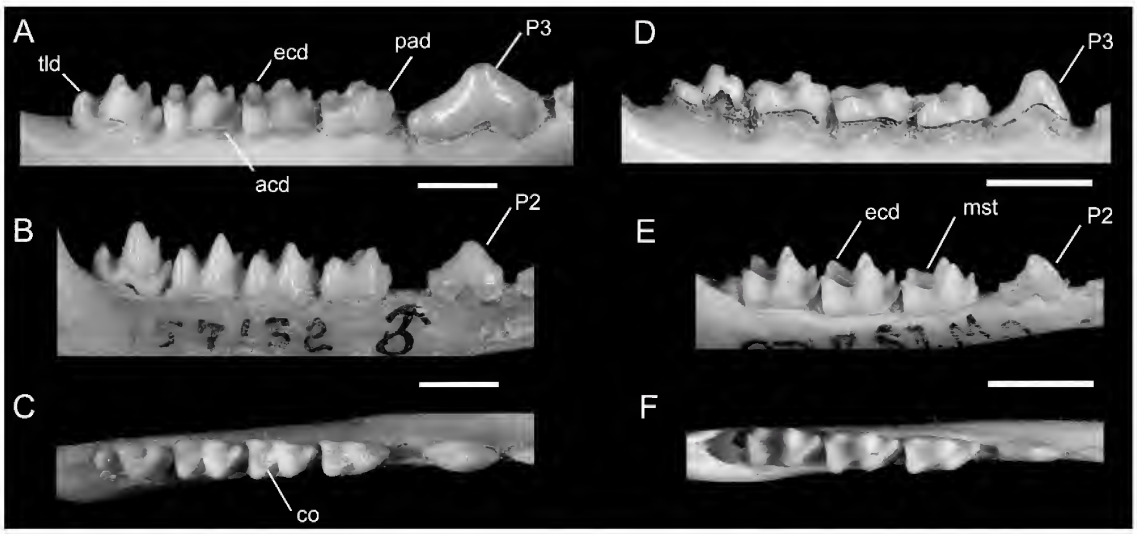

FIGURE 11. Views of the right lower molar series of the two species of *Peroryctes*: **A.** AMNH 157134, *P. broadbenti,* male with P3 and M1–4 fully erupted, in lateral view; **B–C.** AMNH 157132, *P. broadbenti,* male with P3 in crypt and M4 partially erupted, in lateral (B) and occlusal (C) views; **D.** CSIRO M8607, *P. raffrayana,* male with P3 and M1–4 fully erupted, in lateral view; **E–F.** CSIRO M12250, *P. raffrayana,* male with p3 and m4 in crypt, in lateral (E) and occlusal (F) views. Scale bars = 5 mm. Abbreviations: **acd,** anterior cingulid; **ecd,** entoconid; **co,** cristid obliqua; **mst,** metastylid; **pad,** paraconid; **tld,** talonid. Premolar homologies are denoted.

separate, more comprehensive account of cranial variation among peramelemorphians (Kear and Aplin, in prep.).

Features that distinguish *Peroryctes* from other genera of New Guinean bandicoots include:

1. Auditory bullae are relatively smaller and do not encroach forward of the glenoid fossa (expanded anterior to glenoid fossa in other taxa; cf. figs. 8, 12);
2. Foramen of transverse sinus canal is situated at anterior end of an elongate, anteromedially directed sulcus (no sulcus in other taxa; foramen of transverse sinus canal is situated further posteriorly; cf. figs. 8, 12);
3. Foramen for the inferior petrosal sinus is enclosed by converging processes of the petrosal and basioccipital bones (unenclosed, a more open slit in other taxa; cf. figs. 8, 12);
4. Paroccipital processes are more elongate and robust (extremely reduced in other taxa; G&F character 5; cf. figs. 8, 12);
5. Upper canine situated on the premaxillary-maxillary suture (located entirely within the maxilla in other taxa; G&F character 12; cf. figs. 6, 12);
6. Lacrimal foramen situated on the lacrimo-maxillary suture (perforates lacrimal bone in other taxa; cf. figs. 5, 12);
7. Foramen rotundum with more elongate lateral bony tube (elongate in all New Guinean bandicoots but less so than in *Peroryctes*; cf. figs. 8, 12);
8. Premaxillae lack "winglike" narial processes (present in all other taxa; G&F character 6 as "lateral wings"; compare figs. 6, 12);

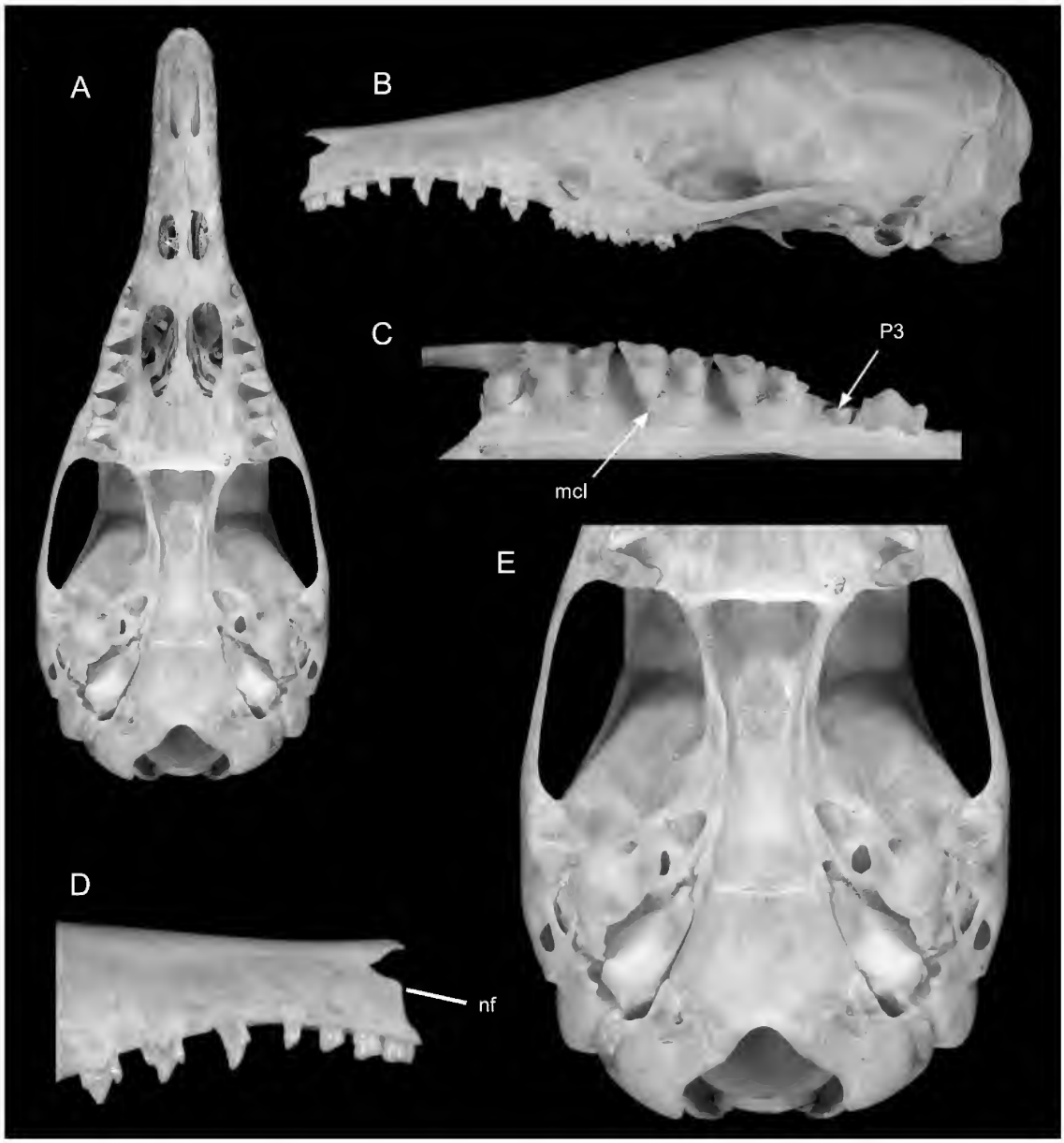

FIGURE 12. Views of the cranium and upper molar series of *Microperoryctes ornata* (CSIRO M15650, a subadult female from Mt Wilhelm, Chimbu Province, Papua New Guinea). **A.** Ventral view of cranium; **B.** lateral view of cranium; **C.** ventrolingual view of upper cheektooth series (tip of unerupted P3 is indicated); **D.** lateral view of rostrum; **E.** ventral view of basicranial region. Abbreviations: **nf,** narial flange of premaxilla; **mcl,** metaconule. Views not to scale (for reference, BCL = 50.3 mm and UML = 9.1 mm).

9. All upper and lower premolars are more elongate relative to molar lengths (cf. figs. 5, 12 and see table 5);
10. Lower premolars with less prominent anterior and posterior cuspids;
11. m4 with less reduced talonid, including less sharply inflected cristid obliqua, more discrete cuspids and broader talonid basin (more reduced in all other taxa);
12. M1–3 metaconules are poorly defined, each cusp separated from protocone by a weak lingual groove (metaconules more discrete in all other taxa; cf. figs. 10, 12);
13. Stylar shelf on M1–3 is incompletely breached between the centrocrista and ectoflexus (*P. broadbenti*) or breached but with remnants of centrocrista retained as enamel "spurs" on M1–2 (*P. raffrayana*) (stylar shelf is completely breached and enamel spurs absent in all other taxa; cf. figs. 10, 12).

Ecological Observations on *P. broadbenti*

Limited information on the ecology of *P. broadbenti* is available from incidental collector's observations, some of which are recorded on specimen labels, and from a few published accounts.

Habitat: The few observations on habitat associations of *P. broadbenti* suggest that the species occurs in dense rainforest habitat and is most often encountered along creeks or rivers. According to Ramsay (1879: 402) the type specimen was obtained "at a considerable distance inland from Port Moresby, in some of the dense mountain scrubs on the banks of the Goldie River." The Sogeri Plateau, the general locality for several captures, supports a mosaic of hill forest and lower montane forest types.

The Peria Creek locality, where members of the Fourth Archbold Expedition obtained the only "series" of *P. broadbenti,* was described in detail by Brass (1956: 137–139). The camp was located "at an elevation of 50 m (or less) on the coastal plain . . . in tall, uninhabited, primary rain forest." The forest

> on the prevailing deep sandy loam and on gentle gravelly ridges . . . had usually a well-spaced stand of the largest trees and numerous big trees of second magnitude which, between them, formed a canopy too complete and shady for any great development of undergrowth layers. Easy to travel through, undergrowth was predominantly woody, of slender small trees, except near streams and in some patches of moist ground where large ferns, aroids, an *Ophiorrhiza,* and big-leaved Zingiberaceae and Marantaceae characterized a luxuriant herbaceous undergrowth.

Brass (1956: 139) mentions the capture of "the giant bandicoot, one specimen of which measured 79 cm from tip to tip and weighed 10½ pounds" and further notes "the light-footed speed they display when startled from cover in the forest." The label of AMNH 157130 specifies that it was "shot crossing streambed."

Reproductive Biology: To our knowledge, only one female with suckling pouch young has been collected—AMNH 157133, with two young, collected on 1 September 1953. However, one other female (BBM-NG 29932) was collected with an accompanying juvenile male (BBM-

TABLE 3. Typical teat numbers in New Guinean bandicoot pouches, as reported by previous workers or observed during this study.

Species	No. of Pairs	Reference
Echymipera clara	3	this paper (AM specimens)
Echymipera davidi	—	not recorded (Flannery, 1990b)
Echymipera echinista	3	Menzies (1990)
Echymipera kalubu	3	Tate (1948b: 320)
Echymipera rufescens	4	Tate (1948b: 320)
Isoodon macrourus	4	Tate (1948b: 320)
Microperoryctes aplini	—	not recorded (Helgen and Flannery, 2004)
Microperoryctes cf. *longicauda*	3	Tate (1948b: 328)
Microperoryctes ornata	2	this paper (AM specimens)
Microperoryctes murina	—	not recorded (Helgen and Flannery, 2004)
Microperoryctes papuensis	2	Aplin and Woolley (1993)
Peroryctes raffrayana	4	this paper (AM specimens)
Peroryctes broadbenti	4	this paper (AMNH specimens)

NG 29930; see table 2 for measurements), and two juveniles (PNGNM 23726, a male, and 23727, a female) were obtained together from Brown River.

Like *P. broadbenti,* almost all Australian bandicoots have four pairs of teats (Tate, 1948b), a condition that is most likely plesiomorphic among bandicoots (Groves and Flannery, 1990). New Guinean bandicoots of the genera *Microperoryctes* and *Echymipera* usually have fewer teats. Here we provide a list of teat numbers for New Guinea bandicoots, when known (table 3). Tate (1948b: 320) was unable to list numbers for most New Guinean species, and Groves and Flannery (1990) incorrectly stated that in *Microperoryctes* and *Echymipera* the teats are "reduced to three pairs." A trend toward reduction in number in these genera certainly is evident, but species of *Echymipera* have three or four pairs and species of *Microperoryctes* have two or three (table 3).

Diet: Menzies (1991: 56) reported that the stomach of one specimen (probably UPNG 557, an adult male) contained only vegetable matter. In general, bandicoots, especially the larger species, are omnivorous (Lee and Cockburn, 1985; Hume, 1999). The dentition of *P. broadbenti* is not unlike that of other New Guinean bandicoots, although the unusual hypertrophy of the premolars in males is exceptional (see below).

DISCUSSION

The Taxonomic Status of *Peroryctes broadbenti*

Despite the former taxonomic confusion surrounding this group, specimens of *Peroryctes* from southeastern Papua New Guinea are readily separable into two distinct groups based on a suite of external and craniodental features. The first group, coming from sites at lower altitudes, comprises large-bodied, harsh-furred animals with plain orange or tan venters; this group includes the holotype of *Perameles broadbenti* Ramsay, 1879. The second group, derived primarily from higher elevations sites, consists of smaller-bodied animals with softer fur and bold white patches on the venter; this group is represented along the entire central mountain

chain of New Guinea and on some of the isolated northern ranges (including the mountains of the Huon and Vogelkop peninsulas and the North Coastal Range), and includes the holotypes of *Perameles raffrayana* Milne-Edwards, 1878, and *Perameles rothschildi* Förster, 1913.

Peroryctes broadbenti and *P. raffrayana* are very distinct species, a fact that was first apprehended in a modern context by Hobart Van Deusen. Earlier muddling of the two species occurred in part because of the rarity of *P. broadbenti* in collections, but was perhaps also due to an intellectual climate that failed to appreciate the enormous mammalian diversity of the island of New Guinea. Van Deusen's insight came from direct experience of both species in the field, coupled with a keen sense of New Guinean ecology and biotic diversity. Whether *P. broadbenti* and *P. raffrayana* are ever found in sympatry is moot, though available records are certainly suggestive of local if not widespread overlap in altitudinal ranges. Clarification of the species boundary should now open the way for more detailed distributional and ecological studies. Ongoing molecular studies also promise to shed light on the degree of genetic relatedness between the two species.

We did not explore the issue of geographic variation within *P. raffrayana*. However, it should be noted that our comparative material includes specimens from throughout the range of this taxon—and that these display a degree of morphological uniformity consistent with the notion of a single, widespread biological species. More detailed studies including molecular assessments are needed to determine whether the geographic forms identified by Tate (1948b) represent valid subspecies.

Our study also stops short of resolving the vexed issue of the relationship of *Peroryctes* with respect to other living bandicoots. As sketched above, *Peroryctes* differs from other New Guinean bandicoots in many aspects of cranial and dental morphology. Unfortunately, with a few exceptions (e.g., characters 1, 4, 11–13), the evolutionary polarity of these features is presently unclear. Working out the cladistic significance of these characters will require much broader comparisons, not only spanning the full range of living and fossil peramelemorphians (including the highly plesiomorphic *Yarala burchfieldi* Muirhead and Filan, 1995) but also extending to members of other marsupial orders. Such analyses should also take into account the considerable interspecific variation within the genus *Peroryctes,* as revealed by the present study.

Sexual Dimorphism in *P. broadbenti* and Other Bandicoots

Sexual dimorphism in bandicoots is variably expressed in terms of overall body size, canine length and robustness, and relative premolar dimensions. Each of these components of sexual dimorphism might provide insights into aspects of the biology of *P. broadbenti* and other bandicoots. Although the following discussion of this phenomenon is not exhaustive, we hope that it will serve to stimulate further interest in this fascinating topic.

Many species of bandicoots exhibit male-biased sexual dimorphism in adult body weight (see table 4). In general, progressively larger species tend to be more strongly dimorphic (fig. 13), a result that is consistent with Rensch's rule, a common scaling pattern in mammals and other animals (Rensch, 1950, 1959). In keeping with this pattern, *P. broadbenti,* the largest species of bandicoot, is also the most highly sexually dimorphic, with males averaging approxi-

TABLE 4. Body weights of reproductively mature males and females of 11 species of bandicoots, primarily based on data recorded on museum labels and in catalogs. Values shown are mean ± one standard deviation, observed range, and sample size. Data for *Macrotis lagotis* are from Southgate et al. (2000) and for *Perameles gunnii* are from George et al. (1990); these are derived from measurement of live animals.

	♂♂	♀♀
Peroryctes broadbenti	4080 ± 800.0 2900–4900 (5)	1170 938–1400 (2)
Echymipera clara	1817 ± 201.4 1650–2100 (3)	978 825–1134 (2)
E. kalubu	1005 ± 294.5 500–1525 (25)	597 ± 120.9 405–820 (16)
Microperoryctes ornata	467 ± 90.7 340–660 (13)	546 ± 147.4 270–670 (10)
M. cf. *longicauda*	745 690–800 (2)	498 395–600 (2)
M. papuensis	154 ± 12.8 136–170 (4)	150 132–167 (2)
Macrotis lagotis	1438 ± 439 range not given (95)	882 ± 169 range not given (89)
Perameles gunnii Tasmania	965.8 ± 260.7 433–1750 (33)	1025 ± 289.0 600–1800 (2)
P. gunnii Mainland	723.0 ± 138.5 466–910 (14)	721.4 ± 123.6 595–881 (6)
P. nasuta	1257 ± 377.0 640–1577 (9)	1005.0 ± 359.2 607–1560 (5)
Isoodon obesulus Tasmania	1544.0 ± 499.4 1134–2100 (3)	872 864–879 (2)
I. obesulus nauticus Nuyts Archipelago	548.0 ± 72.9 490–630 (3)	407.0 ± 28.9 390–440 (3)
I. macrourus	1781.0 ± 661.2 920–2600 (18)	1041.0 ± 357.6 650–1613 (8)

mately 3.5 times the body weight of females. Among the remaining genera of bandicoots, mean weights of males are approximately 1.5–2 times those of females in species of *Echymipera, Isoodon,* and *Macrotis.* In contrast, species of *Perameles* show little or no sexual dimorphism in body weight, even though they equal or exceed the smaller species of *Echymipera* and *Isoodon* in mean male body weight. Possible deviation from the general pattern is also found within the genus *Microperoryctes,* with one species (*M.* cf. *longicauda*) showing male-biased sexual dimorphism, one showing no clear dimorphism (*M. papuensis*), and one possibly showing female-biased dimorphism (*M. ornata*), all within a small overall size range (fig. 13).

Male *Peroryctes broadbenti* do not show any obvious enlargement of the canines compared with females and in this respect they are comparable to most other New Guinean bandicoots. However, marked male-biased dimorphism in canine size is observed in at least one New

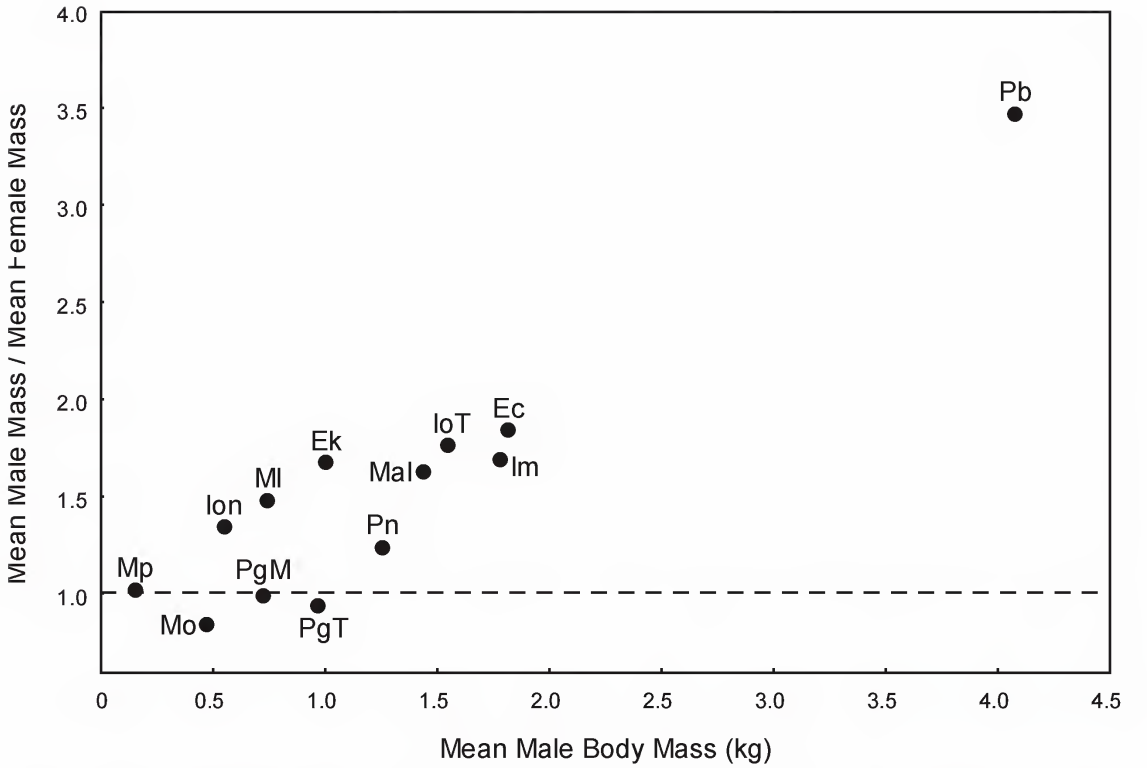

FIGURE 13. Graph of mean body mass (kg) of males against the ratio of mean male/mean female body mass for a variety of New Guinean and Australian bandicoot species. The graph illustrates overall agreement with Rensch's Rule. Data used to construct this figure are contained in table 4. Taxon abbreviations: Ec: *Echymipera clara*; Ek: *Echymipera kalubu*; Im: *Isoodon macrourus*; Ion: *Isoodon obesulus nauticus*; Iot: *Isoodon obesulus* (Tasmanian population); Mal: *Macrotis lagotis*; Ml: *Microperoryctes* cf. *longicaudata*; Mo: *Microperoryctes ornata*; Mp: *Microperoryctes papuensis*; Pb: *Peroryctes broadbenti*; PgM: *Perameles gunnii* (mainland population); PgT: *Perameles gunnii* (Tasmanian population); Pn: *Perameles nasuta.*

Guinean bandicoot (*Echymipera clara* Stein, 1932) and is also present in various Australian bandicoots including *Macrotis lagotis* (Reid, 1837), most if not all species of *Isoodon* (e.g., *I. obesulus* [Shaw, 1897], *I. macrourus* [Gould, 1842]), and some species of *Perameles* (pronounced in *P. nasuta* É. Geoffroy, 1804; less marked in *P. gunnii* Gray, 1838; minimal or absent in *P. bougainville* Quoy and Gaimard, 1824).

The cheektooth row of male *P. broadbenti* is dominated by the oversize P3 (figs. 5, 6, 11). This condition was apparently overlooked by Tate (1948b), despite the fact that he commented on P3 enlargement in two other species of bandicoots—*Echymipera clara* of northern New Guinea and *Rhynchomeles prattorum* of Seram. Curiously, Tate (1948b) did not remark on the sexually dimorphic aspect of P3 enlargement in either taxon. Flannery (1990b) noted male-biased sexual dimorphism in the P3 of *E. clara* and postulated that the same condition might pertain in *E. davidi,* a taxon represented in museum collections exclusively by males but with the P3 proportionally much enlarged over P2 in both upper and lower dentitions.

We have examined specimens of both sexes of all but a few currently recognized species of bandicoots (exceptions include the recently extinct *M. leucura* [Thomas, 1887] and the

TABLE 5. Summary statistics of selected cranial, lower molar, and premolar dimensions of *Peroryctes broadbenti* and a selection of other New Guinean bandicoots, documenting the extent of sexual dimorphism in each taxon (based on adult specimens available at CSIRO and AM). Paired comparisons that are significantly different ($p < 0.05$) under a two-way ANOVA model are indicated by **bold** script.

	Sex	*n*	LMR	LPR	p1L	p2L	p3L
Peroryctes broadbenti	♀♀	1–2	17.1–17.2	14.5	2.8–2.9	3.9–4.0	4.9
	♂♂	6	17.94 ± 0.23	17.88 ± 0.74	3.40 ± 0.26	4.14 ± 0.23	7.06 ± 1.08
Echymipera kalubu	♀♀	33	**13.75 ± 0.57**	**9.82 ± 0.56**	2.15 ± 0.18	2.71 ± 0.17	**3.33 ± 0.35**
	♂♂	55	**14.62 ± 0.57**	**11.55 ± 1.25**	2.23 ± 0.16	2.77 ± 0.19	**3.83 ± 0.37**
Echymipera clara	♀♀	5–6	13.20 ± 0.90	**10.73 ± 1.12**	2.08 ± 0.13	2.55 ± 0.18	**3.42 ± 0.21**
	♂♂	13	13.45 ± 0.71	**12.56 ± 0.82**	2.27 ± 0.16	2.73 ± 0.12	**5.20 ± 0.48**
Echymipera davidi	♂♂	5–6	14.32 ± 0.34	11.84 ± 0.83	2.29 ± 0.06	2.53 ± 0.20	4.57 ± 0.35
Echymipera rufescens	♀♀	9	**13.75 ± 0.65**	**10.56 ± 0.76**	**2.12 ± 0.11**	**2.53 ± 0.12**	**2.92 ± 0.22**
	♂♂	14	**14.67 ± 0.67**	**12.93 ± 1.06**	**2.33 ± 0.18**	**2.79 ± 0.14**	**3.75 ± 0.27**
Peroryctes raffrayana	♀♀	23	15.05 ± 0.79	**12.62 ± 0.93**	2.96 ± 0.21	**3.52 ± 0.25**	**3.57 ± 0.26**
	♂♂	23–24	15.13 ± 0.83	**13.95 ± 0.93**	2.88 ± 0.39	**3.72 ± 0.20**	**3.87 ± 0.36**

insular endemic *E. davidi* [females still unknown]) and can report that P3 hypertrophy is restricted to males of three or four taxa: *P. broadbenti, E. clara, R. prattorum,* and potentially *E. davidi.* However, measurements taken on individual lower premolars and each of the lower premolar and molar series for large series of *E. clara, E. rufescens, E. kalubu,* and *P. raffrayana* show interesting patterns of male-biased sexual dimorphism that includes P3 enlargement (table 5). In *E. clara,* p3 length and the combined length of p1–3 both show extreme male-biased sexual dimorphism. Mean lengths for p1, p2, and m1–4 are slightly larger in males than females, but the differences are not statistically significant. In *E. kalubu,* moderate but statistically significant male-biased sexual dimorphism is observed in lengths of m1–4, p3, and p1–3, with nonsignificant contrasts in mean lengths of p1 and p2. *Echymipera rufescens* shows significant male-biased sexual dimorphism in all of these measurements. Finally, *P. raffrayana* shows significant male-biased sexual dimorphism in lengths of p2, p3, and the combined p1–3, with mean length of m1–4 also slightly larger in males. As illustrated in figure 14, the degree of enlargement of p3 is very similar in *P. broadbenti* and *E. clara,* and possibly slightly less pronounced in *E. davidi.* These plots also give emphasis to the distinctive premolar gradient in *P. raffrayana* in which p2 and p3 are approximately the same lengths (contra p3 > p2 in all other taxa).

While it may be significant that the most extreme P3 hypertrophy in males is present in the two largest-bodied and overall most sexually dimorphic bandicoots, it is nonetheless clear that this phenomenon cannot be explained solely in terms of large body size. One reason is that premolar gradients in female bandicoots show no association between relative P3 size and body size. Another is that males of *Isoodon macrourus* and *Macrotis lagotis,* both of which equal *E. clara* in mean adult body weight, do not show any sign of P3 hypertrophy.

Male-biased sexual dimorphism is far more common than female-biased dimorphism in mammals (Ralls, 1976) and it is usually attributed to sexual selection favoring larger males

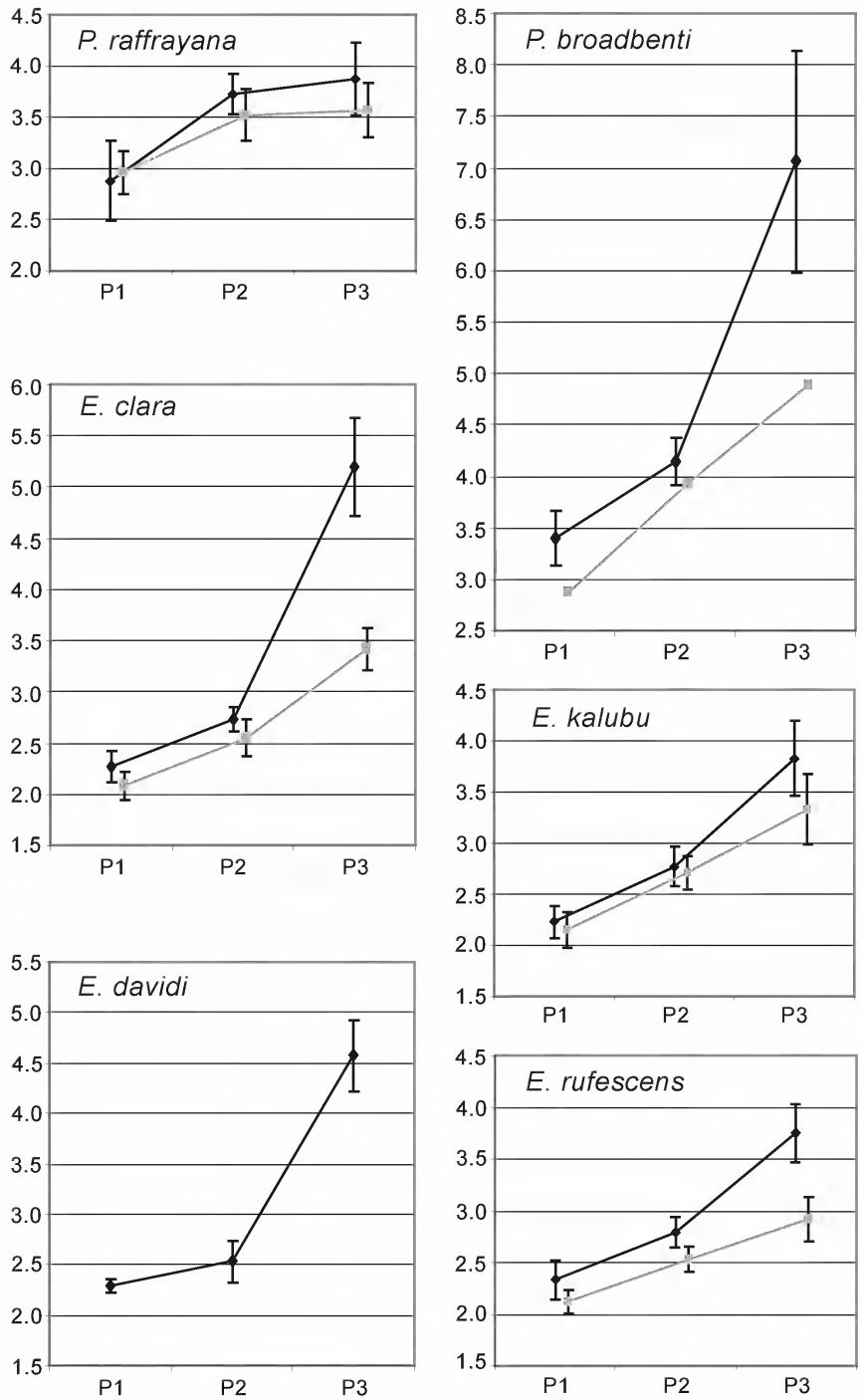

FIGURE 14. Graphs illustrating the variable expression of male-biased sexual dimorphism in lower premolar lengths among six New Guinean bandicoot species (graphs labeled individually). Plotted values are mean and ± one standard deviation, with separate values for males (diamonds) and females (squares) of each species except *E. davidi* for which all known specimens are male. Data used to construct this figure are contained in table 5.

(Darwin, 1871; Andersson, 1994). However, as reviewed by Isaac (2005), detailed studies of mating success have not always confirmed higher reproductive success for larger males in sexually dimorphic species. Instead, these studies point to more complex interplay of factors underpinning sexual dimorphism, including the degree of continuity of breeding through a typical year (larger males are not necessarily more successful during a short breeding season; see Isaac and Johnson, 2003), patterns of resource availability (periods of food scarcity seem to differentially constrain male growth rates; see Le Blanc et al., 2001), and physiological costs associated with growing to, and sustaining larger body sizes (e.g., increased parasite loads, see Moore and Wilson, 2002).

Sexual dimorphism in canine size is commonly associated with polygynous breeding systems in which antagonistic behavior plays a major role in winning or defending access to mates (see Plavcan, 2001; Thorén et al., 2006). Among primates, the most intensively studied group of mammals in this respect, canine size is also correlated with body size, with this relationship expressed in both sexes (Harvey et al., 1978; Greenfield, 1992; Thorén et al., 2006). The presence of enlarged canines in males of some Australian bandicoots (e.g., species of *Perameles* and *Isoodon*) is consistent with the reported significance of male-male competition for mates in these taxa (Seebeck, 2001). However, the apparent lack of such competition in *Macrotis lagotis* (Johnson and Johnson, 1983), a taxon with pronounced sexual dimorphism in canine size, suggests that other factors are probably at play, as does the lack of canine dimorphism in *Peroryctes broadbenti,* despite the extreme contrast in adult body size between males and females of this species. One obvious possibility is that the canines in some groups of bandicoots are important in foraging or feeding behavior. Further speculation is unwarranted until more basic information becomes available on the reproductive and feeding biology of New Guinean bandicoots.

Posterior premolar hypertrophy in male bandicoots is a more obvious pointer to sex-biased dietary specialization, as the enlarged upper and lower P3 of males could serve little purpose in antagonistic behavior. Presumably these massive teeth are used to break open some highly resistant food items such as hard-shelled seeds, thus providing access to food resources that are unavailable to females. In this regard, it is interesting to note that p3 length in male *P. broadbenti* and other bandicoots (table 5) typically shows much higher variance than either of P1 or P2—perhaps indicating a sex-linked morphogenetic system with a high level of instability.

Geographic and Faunistic Context of *Peroryctes broadbenti*

New Guinea's southeastern peninsula (the "Papuan Peninsula" or "Bird's Tail") is an area of moderate mammal diversity but notable mammalian endemism. Reduced diversity in the south-east relative to central New Guinea results from the fact that many montane species that are relatively widespread along the Central Cordillera (e.g., *Murexia habbema* [Tate and Archbold, 1941], *Neophascogale lorentzii* [Jentink, 1911], *Thylogale browni* [Ramsay, 1877], *Baiyankamys shawmayeri* [Hinton, 1943], *Pseudohydromys fuscus* [Laurie, 1952], *Abeomelomys sevia* [Tate and Archbold, 1935], *Mammelomys lanosus* [Thomas, 1922], *Rattus steini* Rümmler, 1935) apparently do not penetrate into the southeastern mountains south of a line approximately delineated by the Angabunga and Bubu rivers in the south and north, respectively

(Flannery, 1995; Van Dyck, 2002; Helgen, 2005b; Helgen and Helgen, 2009). However, certain relatively widespread species that do not extend to the southeast (such as *Coccymys shawmayeri* [Hinton, 1943], and *Pseudohydromys ellermani* [Laurie and Hill, 1954]) are seemingly replaced there by endemic congeners (*Coccymys kirrhos* Musser and Lunde, 2009; *Pseudohydromys germani* [Helgen, 2005a] (see Musser and Lunde, 2009; Helgen and Helgen, 2009), and the lack of records of some widespread New Guinean taxa in the southeast may yet prove to be an artifact of incomplete survey efforts. Eleven mammal species (including one monotypic genus) are currently known only from the southeastern peninsula of New Guinea—one dasyurid (*Murexia rothschildi* [Tate, 1938]), two bandicoots (*Microperoryctes papuensis* and *Peroryctes broadbenti*), seven murine rodents (*Chiruromys forbesi* Thomas, 1888, *Chiruromys lamia* [Thomas, 1897], *Coccymys kirrhos* Musser and Lunde, 2009, *Leptomys paulus* Musser et al., 2008, *Pseudohydromys berniceae* Helgen and Helgen, 2009, *Pseudohydromys germani* [Helgen, 2005a], and *Rattus vandeuseni* Taylor and Calaby, 1982), and an endemic genus and species of vespertilionid bat (*Pharotis imogene* Thomas, 1914), as reviewed in greater detail by Musser et al. (2008). Of the seven endemic murids, four have been discovered or identified as distinct species only within the last several years (Helgen, 2005a; Musser et al., 2008; Musser and Lunde, 2009; Helgen and Helgen, 2009), suggesting that a good deal of additional field and systematic study will be necessary to fully characterize this distinctive regional mammal fauna.

Mammal species that occur in southeastern New Guinea may be classified into several broad ecological categorizations according to their habitat associations, as outlined below (many of these species exhibit slightly different habitat or altitudinal associations outside southeastern New Guinea):

1. Species largely confined to relatively dry and open lowland habitats (such as grassland, woodland, and open forest) below about 500 m (such as *Planigale novaeguineae* Tate and Archbold, 1941, *Isoodon macrourus, Macropus agilis* [Gould, 1842], and *Saccolaimus mixtus* Troughton, 1925);
2. Species largely confined to lowland rainforest and hill forest below about 1000 m (such as *Dorcopsis luctuosa* [D'Albertis, 1874], *Spilocuscus maculatus* [É. Geoffroy, 1803], *Pseudochirulus canescens* [Waterhouse, 1846], *Chiruromys forbesi,* and many bats). *Peroryctes broadbenti* belongs in this category;
3. Species largely confined to hill forests from about 500 to 1500 m (such as *Dorcopsulus macleayi* [Miklouho-Maclay, 1885], *Leptomys elegans* Thomas, 1897, *Microhydromys argenteus* Helgen et al., 2010, and *Macruromys major* Rümmler, 1935);
4. Species largely confined to montane forest at and above 1200 m (such as *Phascolosorex brevicaudata* [Rothschild and Dollman, 1932], most pseudocheirids, *Mallomys aroaensis* (De Vis, 1907), *Coccymys kirrhos* Musser and Lunde, 2009, and *Pipistrellus collinus* Thomas, 1920);
5. Species largely restricted to subalpine habitats (such as *Thylogale calabyi* Flannery, 1992, and perhaps *Mallomys istapantap* Flannery, Aplin, and Groves, 1989);
6. More versatile montane species with a wide altitudinal range, usually occurring above about 400–500 m (such as *Zaglossus bartoni* [Thomas, 1907], *Dendrolagus dorianus* Ramsay, 1883, and *Peroryctes raffrayana*).

Among southeastern New Guinea's 11 endemic mammals (as recognized above), eight are montane species that on current evidence fall into categories 3 and 4. Among lowland species, only three endemics are represented: *Pharotis imogene,* one of New Guinea's rarest bats, known only from sclerophyll woodlands in Central Province (Flannery, 1995); the murine *Chiruromys forbesi,* an arboreal forest-dweller, the range of which also extends to some of the offshore East Papuan Islands (Flannery, 1995; Musser and Carleton, 2005); and *P. broadbenti,* an apparent denizen of dense lowland rainforest and hill forests. Why are there so few lowland endemics in the region? The principal reason may be that relevant habitats (both open and closed forests) are available throughout much of southern New Guinea. Most species that occupy habitats similar to *P. imogene, C. forbesi,* and *P. broadbenti* in southeastern New Guinea have distributions that extend far to the west, often including Gulf and Southern Highlands provinces of Papua New Guinea (Musser et al., 2008; Helgen et al., 2010), the southern lowlands and Trans-Fly region of south-central New Guinea, and in some cases, the land bridge Aru Islands (Flannery, 1995; Aplin and Pasveer, 2005). Further, both *Pharotis imogene* and *P. broadbenti* are rarely collected species, and may yet be shown to occur elsewhere in New Guinea, especially south of the Central Cordillera.

Bandicoot species richness probably reaches its global zenith in southeastern New Guinea. Along a transect running from the vicinity of Port Moresby up to Kagi at 1500 m in the Owen Stanley Range, as many as seven different bandicoot species might be encountered (*Peroryctes broadbenti, Isoodon macrourus, Echymipera rufescens, E. kalubu, P. raffrayana, Microperoryctes ornata,* and *M. papuensis*), as demonstrated especially by series at the AMNH (e.g., Tate, 1948b; Aplin and Woolley, 1993). A similar transect anywhere else in New Guinea (e.g., along the northern margins of the middle part of the Central Cordillera) would probably reveal a maximum of six bandicoots (in this case *Echymipera clara, E. rufescens, E. kalubu, P. raffrayana,* and one or two species of *Microperoryctes*; Helgen, 2007). Across its range, *P. broadbenti* probably occurs syntopically with up to three or four other bandicoots (*P. raffrayana, E. kalubu, E. rufescens,* and *I. macrourus,* all of which are recorded from the vicinity of the Sogeri Plateau), though each of these species has slightly different habitat preferences and associations (Flannery, 1995), and all five would thus be unlikely to occur in the exact same local habitat and altitude.

The interaction between *Peroryctes raffrayana* and *P. broadbenti* has an interesting analog in the biogeographic association between the wallabies *Thylogale browni* and *T. brunii* [Schreber, 1778]. Across their ranges, each of *P. raffrayana* and *T. browni* are primarily species of low to midmontane forests. North of the main body of the Central Dividing Ranges in north-central New Guinea, in the absence of congeners, both species occur down to near sea level in some areas and their ranges include both the North Coast Ranges and the land-bridge island of Yapen (Flannery, 1995; Helgen, 2007). In contrast, in southeastern New Guinea each of *Peroryctes* and *Thylogale* is represented by species pairs that are either altitudinally parapatric or marginally sympatric at intermediate altitudes, with *P. broadbenti* and *P. raffrayana* probably overlapping sympatrically in the Kokoda Trail area between about 400–1000 m, and *T. brunii* and *T. browni* possibly both occurring on the Karimui Plateau at 1000–1600 m (Flannery, 1992). The geographic correspondence between these situations is not exact; for example, *Thylogale browni,* unlike *P. raffrayana,* is not yet known to occur in the mountains of southeastern New Guinea south of the Bubu River.

Several additional examples of altitudinal parapatry or marginal elevational overlap between closely related species pairs are observed in southeastern New Guinea. One concerns the murine genus *Leptomys* Thomas, 1897, with *L. elegans* occurring in hill forest contexts in Northern, Milne Bay, and Central provinces (occurring from near sea level to 1500 m) and the montane congeners *L. ernstmayri* Rümmler, 1932, and *L. paulus* in higher elevation forests in the Owen Stanley Ranges (ca. 1200 m and higher; Musser et al., 2008). Another involves the wallaby genus *Dorcopsulus* Matschie, 1916, with *D. macleayi* recorded from lower montane forests in Central and Milne Bay provinces up to at least 1700 m (Tate, 1948a; Cole et al., 1997), and *D. vanheurni* above about 1000 m and above in the same areas. Similar to the case of *P. broadbenti,* which was often confused with *P. raffrayana* in the past, in several of these examples the two species involved have only recently been distinguished (for *Thylogale,* see Flannery, 1992; for *Leptomys,* see Musser et al., 2008). Additional discoveries of currently undiagnosed, elevationally stratified biological species pairs can be expected in many other Melanesian mammal genera in the future.

Conservation Issues

Evaluating the conservation status and outlook for *Peroryctes broadbenti* has been difficult in the past, both because of previous taxonomic confusion (Seri, 1992) and because so little relevant biological information is available for the species (Leary et al., 2008). As summarized above, essentially all that is known about the biology of *P. broadbenti* is based on museum specimens, the majority of which were collected more than half a century ago. Apart from one recently obtained ear clip, we are not aware of any new specimens of *P. broadbenti* collected in more than three decades, nor has any new information on its biology come to light. The scarcity of historical records for the species suggests it may be a naturally rare animal, and the fact that it was sold in markets in the Port Moresby area in the late 1960s and early 1970s (see above) confirm that it is hunted for food. Hunting pressure apparently led to the local extinction in the Port Moresby area of the macropodids *Macropus agilis* and *Thylogale brunii* by about the middle of the 20th century (Flannery, 1992, 1995). After that time, these kangaroos evidently were replaced in local markets by smaller game, especially the wallaby *Dorcopsis luctuosa* (Flannery, 1992, 1995) and, judging from the various specimens purchased in Koki Market, perhaps also *P. broadbenti,* which is the size of a small wallaby. As the largest-bodied bandicoot, *P. broadbenti* may also be the slowest breeding, which would make it especially vulnerable to declines in the face of overhunting. In addition to human hunting, we suspect that it is also vulnerable to predation by feral dogs and cats. In Australia, bandicoots have proven highly susceptible to rapid declines in the face of various anthropogenic disturbances, including introduced predators and land-use changes (Johnson, 2006; Van Dyck and Strahan, 2008). Within the past century, at least three Australian species (*Chaeropus ecaudatus, Macrotis leucura,* and *Perameles eremiana*) have become extinct, and nearly all Australian taxa have suffered drastic historical range contractions (Seebeck et al., 1990; Van Dyck and Strahan, 2008). With the possible exception of *P. broadbenti,* New Guinean bandicoots appear not to have suffered similar historical declines to date, although subfossil deposits from the broader region record the

apparent extinction during the Holocene of unnamed endemic bandicoots both from Halmahera in the North Moluccas (Flannery et al., 1995) and from the Aru Islands (Aplin and Pasveer, 2005).

Apart from Central Province, available records of *P. broadbenti* cluster in two discrete geographic areas, situated in Oro Province and Milne Bay Province. Large-scale oil-palm plantation operations are underway in both areas (the Popondetta area, Northern Province, and the Alotau area in Milne Bay), resulting in increasing clearance of lowland forest and riparian vegetation along major rivers (World Rainforest Movement, 2001; Shearman et al., 2008, 2009), which we suggest is prime habitat for *P. broadbenti.* Pollution of river systems may be also an issue—one large plantation in Northern Province has faced accusations from local landowners of allegedly disposing of toxic wastes in the Amboga River (Barnett, 2004), one of only two areas in the province where *P. broadbenti* has been recorded (fig. 1).

Like hunting, conversion of lowland forest for oil-palm production (and other stresses associated with the industry, such as riparian pollution and increased local human populations) probably represents a direct threat to the survival of *P. broadbenti.* Leary et al. (2008) recently classified *P. broadbenti* as "endangered" based on IUCN Red List criteria (Schipper et al., 2008), an assessment with which we agree. Given the species' seeming rarity, the lack of recent records, the threats posed by bushmeat hunting and forest clearance, and the historical precedents for bandicoot extinctions throughout Australasia, *Peroryctes broadbenti* must be considered a pressing research priority for conservation biologists working in Melanesia. Attention is urgently needed to better understand the current distribution, habitat preferences, reproductive ecology, and conservation status of this most remarkable bandicoot.

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APPENDIX

List of Museum Specimens Included in Analysis of Body Size Sexual Dimorphism

Microperoryctes papuensis
Females: BBM-NG 109383, BBM-NG 109579; Males: AM M27992, AM M27906, BBM-NG 109408, BBM-NG 109600.

Microperoryctes ornata
Females: AM M17113, AM M21899, AM M17116, AM M28162, AM M13495, AM M17115, AM M16703, CSIRO M15659, CSIRO 15656; Males: AM M16702, AM M20692, AM M15668, AM M17106, AM M17427, AM M15670, BBM-NG 52346, BBM-NG 104239, BBM-NG 109386, BBM-NG 161031, CSIRO M8511, CSIRO M15658, CSIRO M16778.

Microperoryctes cf. *longicauda*
Females: AM M30723, AM M27313; Males: AM M30730, AM M30734.

Echymipera kalubu
Females: AM M13735, AM M17112, AM M29277, AM M29275, AM M28695, AM M28693, AM M28608, AM M17627, AM M15362, CSIRO M8656, CSIRO M8301, CSIRO M8399, CSIRO M8304, CSIRO M8405, CSIRO M8352, CSIRO M8301; Males: AM M13938, AM M13868, AM M13731, AM M29273, AM M28694, AM M18448, AM M14819, AM M21848, AM M20459, AM M29216, AM M17209, AM M14585, AM M13374, CSIRO M8327, CSIRO M8335, CSIRO M8415, CSIRO M8413, CSIRO M8412, CSIRO M8394, CSIRO M8379, CSIRO M8416, CSIRO M8404, CSIRO M8278, CSIRO M8174, CSIRO M8439.

Echymipera clara
Females: AM M15993, AM M13498; Males: AM M14596, AM M23001, AM M14588.

Peroryctes broadbenti
Females: AMNH 157133, AMNH 157135; Males: AMNH 157130, AMNH 157131, AMNH 157134, UPNG 557.

Isoodon macrourus
Females: CSIRO M6054, CSIRO M16380, CSIRO M2998, CSIRO M15288, CSIRO M477, CSIRO M15333, CSIRO M8880, CSIRO M2537; Males: CSIRO M16317, CSIRO M24373, CSIRO M3816, CSIRO M725, CSIRO M800, CSIRO M5790, CSIRO M794, CSIRO M5, CSIRO M6053, CSIRO M7117, CSIRO M15291, CSIRO M1196, CSIRO M24373, CSIRO M533, CSIRO M7121, CSIRO M2538, CSIRO M15478, CSIRO M1196.

Isoodon obesulus nauticus
Females: SAM M8657, SAM M8265, SAM M8266; Males: SAM M8269, SAM M8268, SAM M8267.

Isoodon obesulus (Tasmania)
Females: CSIRO M15836, SAM M7257; Males: CSIRO M15835, CSIRO M6836, SAM M7258.

Perameles nasuta
Females: CSIRO M6245, CSIRO M16320, CSIRO M253, CSIRO M1630; Males: CSIRO M107, CSIRO M13447, CSIRO M6243, CSIRO M10809, CSIRO M24433, CSIRO M10808, CSIRO M3823, CSIRO M16807, CSIRO M144, CSIRO M375.

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